PENNSYLVANIA

Game News

SEPTEMBER 1952 SPECIAL ISSUE NO. 5

TO THE HUNTERS OF PENNSYLVANIA

PREDATOR control is big business in Pennsylvania. Since 1915, at least $5,000,000 of the sportsmen's money has been spent in an effort to produce greater game crops by destroying predatory animals.

Today, many of Pennsylvania's hunters believe that more intensive control is desirable. They are demanding that a determined effort be made to kill even greater numbers of these animals and are convinced that "the only good hawk is a dead hawk."

But wildlife management is a science, and predators form an important part of the wild life of the state. Therefore, it is the responsibility of the Pennsylvania Game Commission to consider predators and predator control from a strictly scientific viewpoint. They are obligated to study the relationships between predators and their prey and attempt to determine their destructive or beneficial qualities. From these studies, they must decide whether control is needed and, if so, where it should begin and where it should end.

The following pages contain a revised report of the findings of some of these research studies. It is believed that the sportsmen of Pennsylvania will welcome the opportunity to make their own independent decisions concerning predators and predator control. For this reason, all specific recommendations have been deleted. It is hoped that the readers will discover that all predators are not bad; that predator control does not always result in increased game populations; and that sometimes predators can actually improve hunting.

Here are the pros and cons of the question, and the information necessary to settle many arguments at the club or hunting camp. Here is an opportunity for the hunters of Pennsylvania to decide whether their license money should be spent for intensive predator control or for other game management methods which may have a greater benefit in the long run.

PENNSYLVANIA Game News

Published Monthly
(Semi-Monthly in September and March)
by the
Pennsylvania Game Commission

Commonwealth of Pennsylvania
JOHN S. FINE, GOVERNOR

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Special Issue No. 5

The Predator Question
By Roger M. Latham

Taken from Final Report II
Pittman-Robertson Project 36-R

The Ecology and Economics of Predator Management

Cover painting by Ned Smith

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RATES—$1.00 for one year, $1.50 for two years, and $2.00 for three years, with a special rate of 50 cents for all resident sportsmen's organizations when such subscriptions are submitted in lots of ten or more. Remittance by check or money order to be made payable to the Department of Revenue, Commonwealth of Pennsylvania, and addressed to Pennsylvania Game Commission, Harrisburg, Pa. CASH FORWARDED AT SENDER'S RISK. STAMPS NOT ACCEPTABLE. Your local Game Protector, County Treasurer, or other Hunting License Issuing Agent will take your subscription; or you may forward it direct to the Pennsylvania Game Commission, Harrisburg, Pa.

Please report all changes of address promptly, sending both your old and new addresses. Address all communications to the Editorial Office, Pennsylvania Game Commission, Harrisburg, Pa.

Entered as second-class matter at the Post Office of Harrisburg, Pennsylvania, under the Act of March 3, 1879. Mailed in conformity with P. O. D. Order No. 19687.

Printed at The Telegraph Press, Harrisburg, Pa.

Permission to reprint will be granted provided proper credit is given.

RED FOX

THE PREDATOR QUESTION

By ROGER M. LATHAM

Taken from Final Report II
Pittman-Robertson Project 36-R

The Ecology and Economics of Predator Management

PUBLISHED BY THE
PENNSYLVANIA GAME COMMISSION
Harrisburg

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Preface

Pennsylvania has paid bounties on one or more presumably noxious animals constantly since 1683. Beginning in 1913, all money paid for bounties by the state has originated from the Game Fund—the revenue received from the sale of hunting licenses. In 1915, the obligation for these payments was transferred from the County Treasurers of the respective counties to a central office in Harrisburg. During the period from 1915 to 1952, the Pennsylvania Game Commission has expended $3,706,457.50 for the control of predaceous birds and mammals as a function of game management.

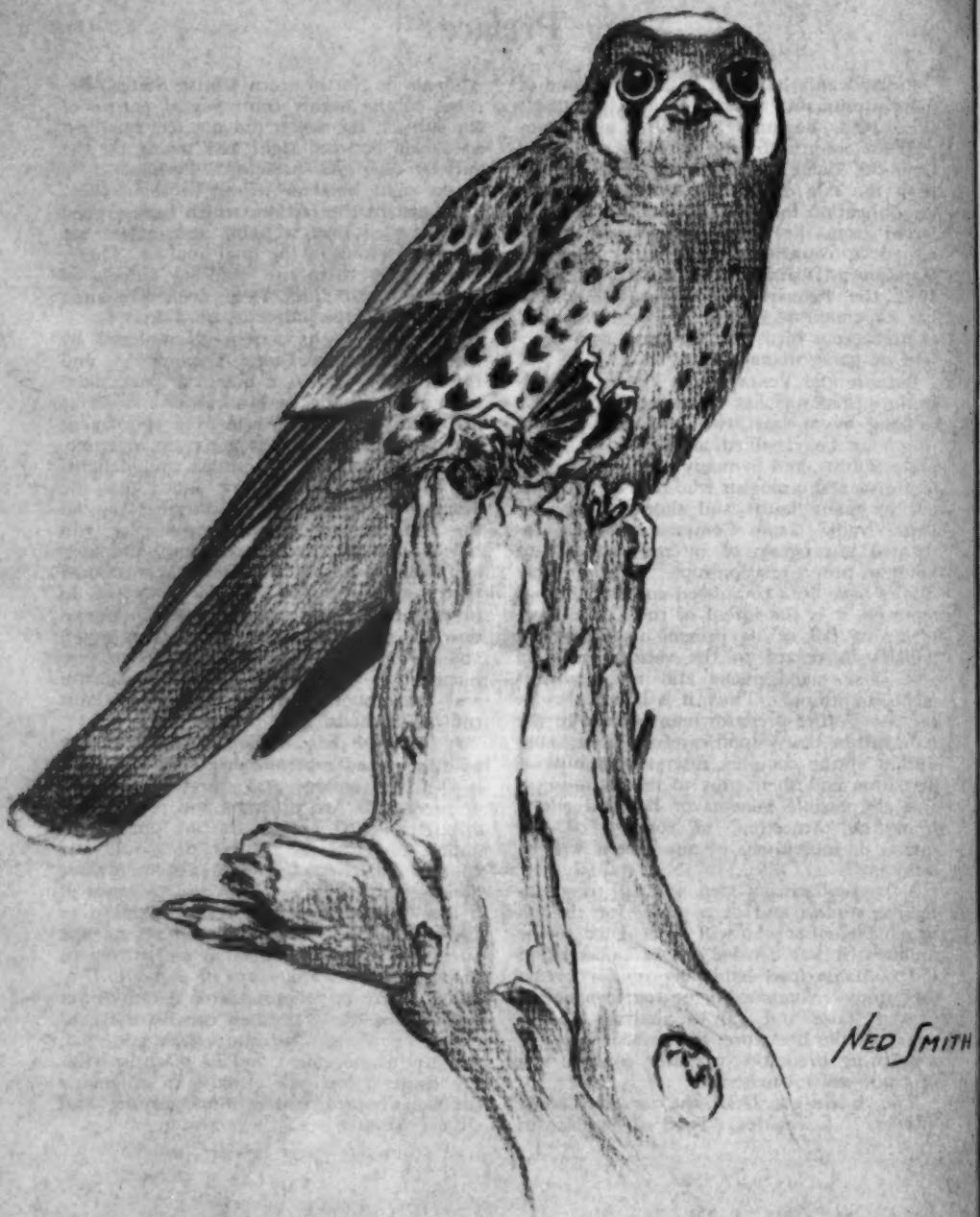
Because the Pennsylvania system of controlling predators has been under attack for so long by at least two factions—by those who may be classified as nature lovers or protectionists, and by many trained economic biologists and ecologists who repeatedly point out its many faults and shortcomings, the Pennsylvania Game Commission wisely instituted a program of intensive studies of predator-prey relationships. When these studies have been completed and the findings reported, it is the intent of the Commission to review all of its present practices and policies in regard to the various pedators and their management and make adjustments accordingly. Thus, it is hoped that in the near future predator management in the state will be based upon carefully interpreted studies of the complex interrelationships of predators and their prey to man's interests, and all possible benefits or harmful effects from the protection, or control, of any species or individuals of any species will be considered.

As a preliminary step toward these intensive studies and as a guide for the research biologists who will be assigned to the problem, it was decided (1) to amass all of the available food habits figures for predatory animals common to the fourteen northeastern states and (2) to analyze, from a search of the literature, the present concepts concerning predators, predator control, and predator control methods.

This is *Report II* of the two-part study (Report I is entitled, "Food of Predaceous Animals in Northeastern United States). Because of the highly controversial nature of the subject, the writer did not feel qualified to decide between right and wrong on the various questions presented. Perhaps there is no right and no wrong in some cases, and perhaps the factions which have argued and haggled over a point year after year are both wrong in the final analysis. Therefore, where there are differing schools of thought, both sides have been presented with as little prejudice as possible.

Vocationally, the writer is employed by the Pennsylvania Game Commission and thinks and works as a practical game manager; avocationally, he is a hunter and fisherman and thinks and acts as a sportsman; and sentimentally, he is a nature lover-seeing beauty in all living things and delighting in their existence. It is hoped that the discussion, based upon an interpretation of the literature and personal experience, will reflect an open mind and an unbiased approach. However, it must be remembered that the basic purpose of the study was to investigate the relationships between predators and valuable wildlife (pincipally game) and to review the present knowledge concerning the advisability of predator control and the economics of the various predator control methods.

It is hoped that this report will stimulate additional and much-needed research. What is the true ecology and the true economy of predation? Are predator and prey mutually dependent? Are we wasting millions of dollars for predator control, or should our efforts and expenditures be even further increased? Should we adopt the "balance of nature" concept and allow our wildlife to adjust itself naturally, or should we manage our game and furbearers as intensively as we manage our farm crops or domestic livestock? There are thousands of questions yet unanswered. Only research can fill the gaps in our knowledge, and, until these are filled, predator management and its place in wildlife conservation will remain an enigmatic function characterized by blind gropings and clumsy blunderings.



SPARROW HAWK

PART I

Predator Food Habits Studies

INTRODUCTION

UNTIL the pioneer studies of Warren (1890) and Fisher (1893), almost nothing was known of the food habits of the various predatory species. Prior to these studies the supposed harmful, neutral, or beneficial nature of an animal's feeding behavior was based almost entirely upon scattered observations. Because there was seldom an instance wherein someone had not observed some individual of almost every predatory species in an act contrary to man's interests, and because no one could state definitely how many times members of a certain species might have repeated a similar misdeed, all predators were condemned and subjected to some degree of control.

Quantitative analyses of stomach contents, fecal droppings, and regurgitated pellets provided something reasonably concrete for ecologists and economic biologists to evaluate the status of the carnivorous animals. Within a short time, certain groups were calling for a cessation of the constant persecution of various birds and mammals which had been, according to them, proven beneficial or harmless by the analytic studies of Warren and Fisher. Even among game men, there was a growing doubt in many minds that blanket control of *all* predators was a desirable practice to increase game populations. As a consequence, food habits research was stimulated in all parts of the country.

For the following three or four decades the economic status of predatory species was based almost solely upon the result of these examinations. If the diet of a particular bird of prey or carnivorous mammal showed a preponderance of desirable or useful prey species, then the animal in question was classified as harmful and was black-listed by game managers. Little or no cognizance was taken of such factors as the relative density of predator and prey populations, the food preferences of the predator, the physical condition of the prey, the amount and location of escape cover, and the abundance and availability of "buffer" species.

During the past 20 to 25 years, greater emphasis has been placed upon the end result of predation—its total effect upon prey populations and upon man's economy—instead of upon the fact that a definite percentage of the diet was composed of a particular prey species. At present, it is fairly well agreed among professional wildlife workers that *food habits figures for predators have comparatively little significance unless accompanied by specific ecological data from the region where the stomachs, scats, or pellets were collected.* In other words, it is almost impossible to evaluate the economic status of a flesh-eating animal from food habits figures alone. The proper interpretation of the occurrence of a prey species in the diet of a predator may have as much significance as its correct identification in food samples in the first place.

Game administrators, agriculturalists, and livestock raisers are inclined to classify predatory animals according to the amount of good or harm they may do in relation to their particular interests. In the past this classification has been derived from an evaluation of food habits tables

which often represented only a few food sample analyses or sight records. The subsequent discussion will deal with the problems which arise when an attempt is made to designate the true role of a predator as it affects the economy of one group or another from the interpretation of food habits figures alone.

PROBLEMS ENCOUNTERED IN ATTEMPTING TO EVALUATE THE ECONOMIC STATUS OF A PREDATORY SPECIES FROM FOOD HABITS STUDIES

Sampling

Inadequate Number of Analyses or Observations

THE meaning here should be fairly obvious. Suppose, as often has been done, only 30 or 40 stomachs of red-tailed hawks, or of some other predatory species, are analyzed for a region, and its good or bad qualities *assumed* from this study. During a greater part of the year, hawks appear to have two major periods of activity daily, although they will overlook few opportunities to feed at any time. For sake of discussion, let us assume that red-tailed hawks, on the average, eat two meals daily. Because digestion is rapid, and because pellets are regurgitated, we may further assume that new food is represented in the stomach each day. Then in a year's time, the stomachs of the 30 redtails mentioned above could contain a total of 10,950 separate collections of food items. Of these 10,950 possible samples, only 30 have been analyzed—less than three-tenths of one per cent. This is hardly adequate sampling!

Similarly, a few dozen scats or pellets may, under certain circumstances, give a distorted picture of the true dietary tendencies of the animal, although scats may often contain the remnants of food items consumed over a period of two or three days. The same logic will apply to observations made at dens and nests where food materials are brought to feed the young.

Thus, it can be seen that limited sampling may be misleading and result in an erroneous designation of the economic status of a predatory species.

Observational studies of food remains at mammal dens and raptor nests are indicative of feeding trends, but the smaller prey items, which often may be swallowed whole, will not appear among the residue. By collecting and analyzing the scats or pellets of the young animals, this deficit may be partially corrected.

Faulty Techniques

(1) *Lack of skill or thoroughness of analyst.* If a technician presents a food habits table showing no unidentified materials, he is either exceedingly skilled, is working with a very simple diet, or is dishonest. But some analysts have an excessively long list of unidentified items, and there is always the possibility that, if the identity of some or all of these were known, the predator's economic position might be considerably altered. This would be particularly true if the unknown items happened to be nearly all the same. For example, quite often the great majority of the birds taken by barn owls are starlings and English sparrows, both of which are usually considered pest species. The finding of house sparrows and starlings, in its pellets would contribute to the "credit" side of the owl's diet, but, if these were

not identified to species, it is likely that they would be charged against the owls since small birds, as a group, are usually considered beneficial. Many more examples could be cited to show that identification of food items should be as complete and specific as possible.

Mis-identification is likely to be even more serious than lack of identification since this could mean a transfer of items from the "debit" side to the "credit" side, or vice versa. There is no need to dwell upon a situation so obviously undesirable.

Incomplete Representation of Diet in Stomachs, Scats, and Pellets

Ordinarily, the items occuring in stomach contents are fairly readily identifiable at least to class and most often to genus or species. Because of the freshness of the material and its ease of identification, stomach analysis would appear to offer the most complete record of the animal diet, but even this method does not reveal the number and kinds of prey killed but not eaten. In the case of some carnivores, the numbers of prey animals killed may be several times as large as the number represented in stomachs or scats. Foxes, minks, weasels, and others are known to kill many (even one, two, or more hundreds in a single night) penned chickens, ducks, ringnecked pheasants, or other birds. A night's carnage of this sort probably would show only as one chicken, one duck, or one pheasant in the stomach. Foxes, coyotes, and other mammals are known to kill several rabbits, pheasants, or other prey in a single night of opportune hunting and to cache most of these, in their entirety, for possible future use.

Some prey species may be killed regularly and discarded uneaten. Foxes seem to have an aversion to the taste or the odor of weasels, moles, and shrews. It may be significant that a pronounced scarcity of weasels coincided with the recent irruption of foxes in Pennsylvania, but, even though foxes may have been responsible for this reduction, very few weasels would appear in fox stomachs collected during this period. This is only a single instance of many possible ones where predator-prey relationships would not be revealed by food habits figures.

Digestion of certain food materials is so complete that recognizable remains cannot be found in fecal samples and pellets. The digestion of very young nestlings of altricial birds and the naked soft-boned young of rabbits, mice, and many other small mammals is usually so complete that no suggestive trace can be found. Other remains, e.g., the shafts and quills of feathers are only identifiable as birds of certain size groups.

If food samples are examined only superficially, as much as one-third to one-half of the total number of items occurring in the samples may be missed. Such hasty, unscientific examinations are usually occasioned by a lack of interest on the part of the analyst, ignorance of proper methods, or insufficient time for a thorough job. Because considerable importance may be attached to any published food habits figures, the science of wildlife management would be benefited more if cursory examinations of this kind had never been made. The old axiom "if a thing is worth doing, it is worth doing well" certainly holds true in this case.

Few technicians have the training and experience necessary to classify them as experts in the laboratory analysis of stomach contents, scats, and pellets. This requires an intimate knowledge of the flora and fauna of the region where the food samples were collected and of microscopic techniques in identification of hair and feathers. One must also be a taxonomist to be able to list properly the animal and vegetable items found, an anatomist to iden-

tify bones, feet, bills, teeth, etc., and a botanist, mammalogist, ornithologist, entomologist, and herpetologist to recognize plant, mammal, bird, insect, reptile, and amphibian remains. In other words, *good food habits technicians are made, not born!*

(2) *Misidentified scats or pellets.* If representative scats from a mink, an opossum, a skunk, a raccoon, a gray fox, a red fox, and a bobcat, each of which had eaten a meal of cottontail rabbit, were placed side-by-side, how many wildlife technicians could correctly name the source of each? Similarly, how many would be capable of distinguishing the pellets of the barn owl, short-eared owl, long-eared owl, barred owl, and great horned owl if these were all composed of nothing but the hair and bones of meadow mice? How many times have the fecal droppings of one or more other species been collected and analyzed as fox scats by undiscerning field workers? Might not this add to or detract from the economic value of a predatory animal?

This is not to infer that technicians regularly produce distorted figures because the source of their series of scats or pellets have been falsely identified, but the possibility of error is mentioned as a note of caution to inexperienced wildlife workers.

(3) *Insufficient data with samples.* It is common failing among cooperators who are furnishing stomaches or other food samples of predators for a study to forget to record the date, the locality where collected, method of taking the animal, bait used (if any), and even the species name. The fact that predator food habits figures are only valid for a specific time and place makes the recording of this information indispensable. If bait is used to trap or poison a predator, the nature of the bait should be listed so that this item can be excluded from the stomach samples, unless it should occur more than once in a stomach.

Many fine series of predator food samples have had to be discarded, or their value has been greatly reduced, because of neglect or forgetfulness on the part of the collector.

Seasonal Variations

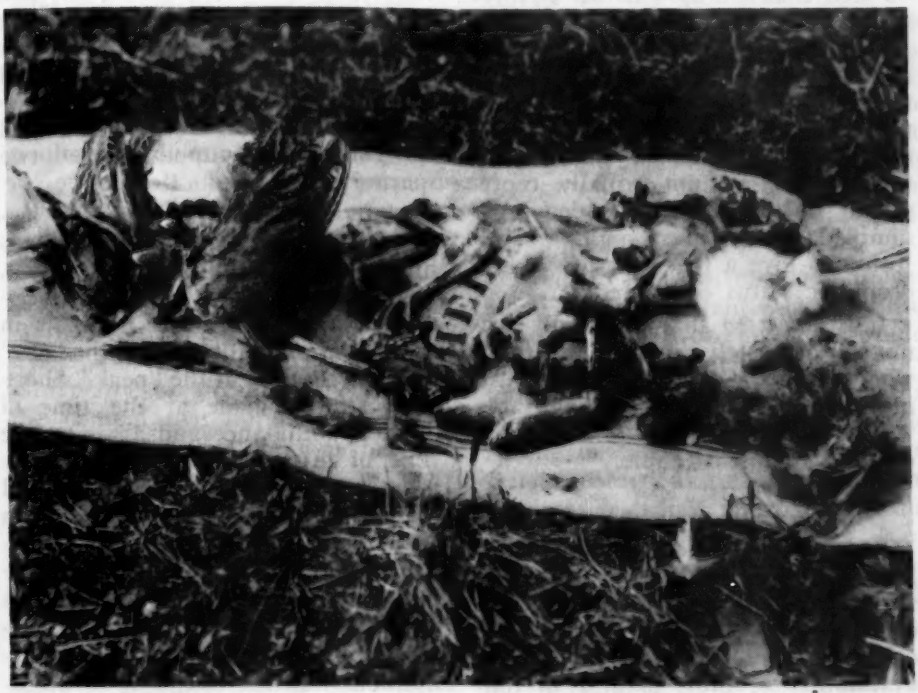
One of the most serious criticisms of predator food habits studies arises from the fact that, in many instances, the investigator will collect and analyze a series of stomachs, scats, or pellets during one or two seasons of the year and publish the results as representing the typical diet of that animal. For many years, almost all of the food analyses for the fur-bearing animals were made for the fall and winter seasons when stomachs were available from animals trapped for their fur. Without a fair sampling from the spring and summer months, the figures told only part of the story, and the economic status of a predator could be greatly changed by the addition of the warm-weather diet. Because of these short-term studies, pressure groups could, with a little search, find and use published figures which most nearly suited their purposes. For instance, fox-hunting clubs have distributed literature to farmers, sportsmen, and other antagonistic groups showing that foxes eat only fruit, insects, and mice on the authority of Joe Jones, wildlife expert from some state at least 500 miles distant.

The broad-winged hawk can be used to illustrate the decided seasonal variation in diet. Broadwings shot in the early fall will almost invariably contain some Orthoptera and Lepidoptera, and most often their stomachs will be distended with these large grasshoppers, katydids, and caterpillars. A series of stomachs collected at this time of the year would certainly classify the broad-wing as decidedly beneficial in its feeding habits. But in the spring

when most insects are comparatively small and many are unavailable, this hawk is forced to eat other types of food. Now small mammals, amphibians, and reptiles are represented regularly, and recent studies (Latham, 1946) indicates that the broadwing may be an important factor in the decimation of juvenile ruffed grouse when the hawk is under the stress of feeding its young. It is possible that the broadwinged hawk and other predatory animals may be almost entirely beneficial during eleven months of the year, but may, during the remaining month, exhibit feeding tendencies inimical to man's interests. Such short-term influences could be easily missed by the wildlife worker unless he collected a substantial year-round sample or was highly observant in the field.

The game manager's quarrel with the crow is confined to the spring and early summer months, except when it occasionally competes with game for winter food. Its condemned habits of destroying eggs, eating fledglings of song birds, killing and eating young game birds and cottontail rabbits, and even pulling corn all coincide with the reproductive activities of spring and early summer. If these unsavory habits were excluded, the feeding habits of the crow for the remainder of the year would be largely beneficial.

The stubborn tenacity of the Cooper's hawk, once it is able to locate a covey of bobwhite quail on deep snow, is often maintained until the covey is annihilated (Latham and Studholme, 1947). Under such circumstances, this hawk may kill one to two quail almost every day for a



PGC Photo by Latham

Material found at predator dens does not necessarily represent a true picture of the animal's diet.

period of a few days to several weeks. Stomachs collected at other seasons of the year, even from the same area, are unlikely to reveal losses of this magnitude.

In the West, the taking of big game animals by eagles is confined to the short period when the tiny young of such animals as antelope, mountain goats, and others are available. The destruction of ducklings by pike and snapping turtles can only occur at one season; muskrats may be most vulnerable to foxes and minks during a season of drought; and the food habits of many species may be greatly changed during plagues of mice and insects. In the far North, arctic foxes feed upon birds and lemmings in summer but subsist upon the remains of seals killed by polar bears and the dung of the bear during the winter.

From the above discussion, it can be seen that the food habits of most predators change with the seasons, particularly in temperate climates, and, unless each of the seasons is represented proportionally, an accurate year-round sample cannot be obtained. It is suggested that, where the seasons are not equally represented but, nevertheless, adequately sampled, the figures might be adjusted to give a truer picture of the economic status of a predator.

It is admitted that the result cannot be completely accurate, but those who criticize a mathematical adjustment cannot deny that the final table will be *more nearly accurate* than the original unadjusted table.

Yearly Variations

Because of the ever-changing population levels of predatory and prey species, because of the effects of drought, snow, excessive rainfall, and other meteorological factors upon the availability of prey, because of natural or artificial alterations of the habitat and the amount of protective cover it may provide, and because of the introduction of exotic species, the diet of predatory animals may vary considerably from year to year.

Food habits studies continued over a period of years for the same species and for the same area will often show widely divergent figures. To illustrate, Luttringer and Sutton (1924-1934) who examined the contents of 538 goshawk stomachs from Pennsylvania found that 31 per cent of the stomachs contained ruffed grouse, 24 per cent contained cottontail rabbits, and 9 per cent gray squirrels. A few years later, McDowell and Langenbach (1937-1940) analyzed the food found in 101 goshawk stomachs from the same state, but found only 13 per cent contained grouse, 15 per cent cottontail rabbits, and 19 per cent gray squirrels. Were grouse and cottontails more abundant during the decade from 1924 to 1934 than they were during the late 30's, were these prey species more readily available because of deeper snows or some other environmental factor, or were other prey items relatively scarce and the hawks forced to concentrate upon these two species?

Many kinds of prey (grouse, varying hares, most mice, and others) exhibit marked population fluctuations. These cyclic species are almost certain to appear in fewer numbers in the diet of predators during the "low" of the cycle than at the "peak." Short-term studies made at the time of greatest abundance and again at the time of least abundance of a cyclic prey animal might produce food habits tables which would indicate a malevolent predator-prey relationship on the one hand and a comparatively benevolent relationship on the other. (But even though a particular prey animal may appear infrequently in the stomachs of predators during the low of the cycle, this does not mean that the pressure is not equally as great, or greater, than

when many individuals are taken during periods of abundance.)

The investigations of Errington (1937) and others have shown that muskrats and other prey animals may be exceedingly vulnerable to predation during periods of drought. Thus, during drought years, the fox, as one example, may become a potent factor in the decimation of muskrat populations but may exert only moderate pressure during more normal years. The literature is full of references to the vulnerability of prey upon deep snows, particularly if these are long-continued. This insecurity is occasioned by a sparsity of concealing cover and is heightened by a physical weakness of the prey resulting from food scarcities. Floods, forest and prairie fires, cultivation, lumbering, and other changes of the environment may create a temporary susceptibility of prey which could alter the food habits of predators.

Even the introduction of new prey species, or the large-scale planting of artificially propagated game, or the establishment of new or expanded poultry or livestock industry in a region may all affect the diet of predatory animals from one year to another.

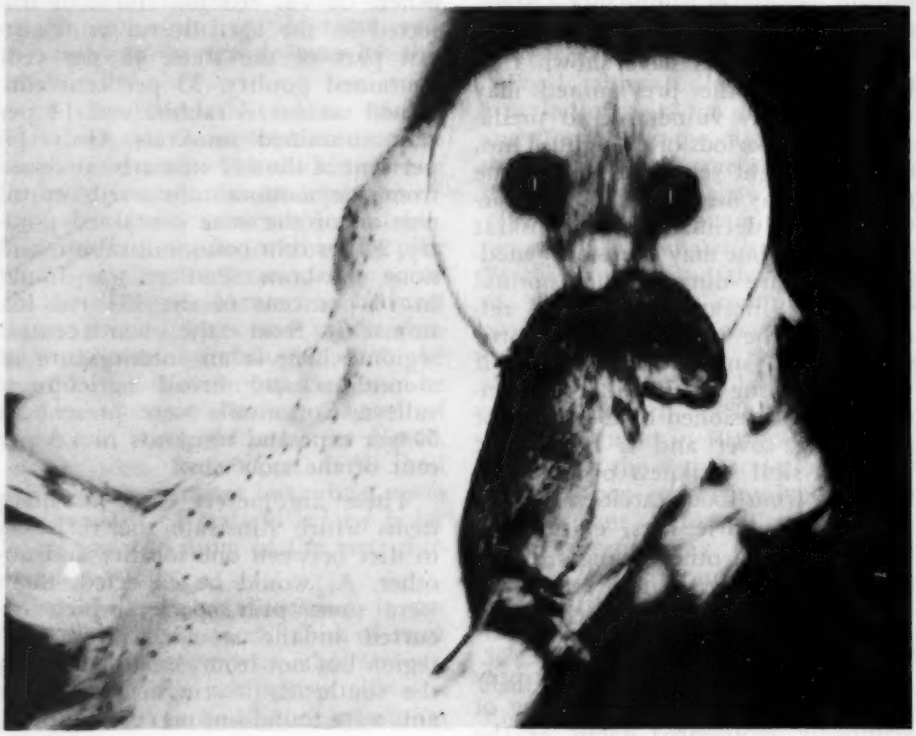
Thus predator food habits studies made in the past cannot safely be applied to the present nor the future. The list of prey items may not contain many, or any, new species, but the comparative importance of the different items in the diet may be altered significantly. This is most likely to be true of predatory animals which select a varied and extensive diet, e.g., foxes, coyotes, Buteo hawks, and others.

Locality Variations

Three separate food habits studies of the red fox in Pennsylvania from three different regions of the state show clearly the variations which can be expected from one locality to another. Of 147 red fox stomachs collected in the agricultural southeastern part of the state, 45 per cent contained poultry, 33 per cent contained cottontail rabbit, and 14 per cent contained muskrats. Only 1.5 per cent of the 147 stomachs analyzed from the mountainous north-central portion of the state contained poultry, 26 per cent cottontail rabbit, and none muskrats. Poultry was found in 16 per cent of the 131 red fox stomachs from the south-central region which is an intermixture of mountains and broad agricultural valleys. Cottontails were present in 50 per cent and muskrats in 1.5 per cent of the stomachs.

These are merely three of many items which illustrate the variances in diet between one locality and another. As would be expected, there were some prey species which occurred in the stomachs from one region but not from the others. From the southeast, 16 ringnecked pheasants were found but no ruffed grouse; from the north-central portion, the analyses revealed 6 grouse but no ringnecks; no ringnecks; and only one grouse was found for the south-central region, but bobwhite quail (2) appeared for the first time.

Even greater discrepancies appear when more distant geographical regions are involved. One would hardly expect the diet of a predatory animal found in South Carolina to be comparable to that of the same species in Maine, but oftentimes differences nearly as great exist between predator diets from forested areas and agricultural areas within the same state or county. Therefore, the same conclusion can be reached in regards to locality variations in diet as for seasonal variations in diet, i.e., that predator food habits are specific as to place and the findings for one locale should never be assumed to apply to any other.



The diet of the barn owl is predominantly beneficial, consisting mostly of mice and other small rodents.

Interpretation

Ecological Data Needed

AS HAS been stated before, no predator food habits table can be interpreted from an economic standpoint without additional knowledge concerning the relationships of the predator and its various prey to the environment and to man's interests. Economically, the occurrence of particular prey items in the diet of a predator means little unless it can be shown by ecological investigations that the predator-prey relationships are desirable or undesirable. The kinds of information needed for intelligent interpretation of predator food habits tables are discussed.

(1) *Availability of prey species.* Within certain limits, availability, above all else, governs the diet of most predatory animals. Most carnivores are opportunists, and, if one prey item does not occur in fair abundance or is not easily captured, it will be replaced on the diet list by other, more readily available prey species, or even by non-prey items such as vegetable matter or carrion.

(a) *Abundance of prey—cyclic species.* It is only logical that when a prey species is abundant, its natural enemies are afforded more opportunities to capture and kill than when the species occurs only sparsely. Predator food habits studies conducted on a specific area and for a number of years are likely to reveal a marked fluctuation in the comparative quan-

tities of the various prey items consumed. This is especially true of cyclic species whose numbers may vary from a "low" phase to an "irruptive" or "plague" phase. The frequency of occurrence of a prey species in a predator's diet is often so closely proportional to the size of the prey population that a continuous examination of stomachs, pellets, or scats over a period of years can be used for determining the length and intensity of the cycle. Barn owl pellets often reveal the presence of species of mice and shrews which even at the peak of the cycle are never common. To attempt to establish the cycle for such rare species by the ordinary census methods (live-trapping or snap-trapping) would certainly involve a great amount of painstaking labor, but owl pellets are likely to give a reasonably accurate picture of the rise and fall of numbers with a minimum of effort.

Because a predator's food intake remains relatively constant in volume, except possibly in the Arctic or during winter, it means that an increased consumption of one item will almost certainly result in a proportional decrease in the quantity of other dietary items even though the population level of many of these may have remained almost static. The discrepancy constitutes the major source of error in the determination of cycles from food habits figures.

(b) *Weather conditions.* Meteorological influences which may affect the availability of prey animals have been mentioned as factors causing seasonal and yearly variations in food habits figures.

Deep snows may expose bobwhite quail and other upland game birds but provide a protective blanket for mice, shrews, and other small animals. During these periods of stress, the diet of a predator may vary considerably from the normal bare-ground diet and may change from beneficial to harmful for the duration of the snow. The goshawk-ruffed grouse and Cooper's hawk-bobwhite quail relationships illustrate the increased vulnerability of certain prey on snow.

Errington (1937), Bennett (1938), Scott (1937), and Kalmbach (1937), and others have shown that drought intensifies predation upon muskrats, ducks, and other aquatic animals. When streams, ponds, and marshes become partially or wholly dry, these animals are denied the usual protection afforded by the water in diving or swimming, and it also permits predatory animals which normally shun water (foxes) to invade the very homes of these birds and mammals.

Drought may also cause an increased susceptibility of prey because of a sparsity of protective vegetation.

Floods may expose prey animals, especially to avian predators, and the sight of a marsh hawk gorging itself on meadow mice over "drowned" meadows is a common sight. Other, less important, weather influences may cause an increased or decreased take of prey items.

(c) *Physical condition of prey.* The natural vigor and ability to escape from predators may be lacking in prey animals which are suffering from malnutrition, exposure, disease, injury, and perhaps other physiological and pathological conditions. There is also the possibility of genetic weaknesses resulting from the mating of northern strains with southern strains which may produce offspring incapable of maintaining top physical quality during cold weather. Sometimes handicaps may be of a mechanical nature (mud-balling, etc.).

Deep snows, ice storms, overbrowsing or over-grazing, the failure of mast crops, extended drought, and other factors may cause a temporary shortage of food and a consequent malnourishment of prey species. Underfed animals are likely to lack the attributes of strength, speed, and

alertness so necessary to prevent capture by predators. The question arises as to whether the capture of prey weakened by a lack of proper food should, or should not, be charged against the predator. The answer appears to be simply that if the prey animals would have survived, had they not been killed, the predators should be held responsible. There are those, however, who will argue that the inadequacy of the habitat is the real cause and that predation is merely a subordinate factor. Probably this thesis is tenable where a prey population is living beyond the true carrying capacity of its food supply and is, therefore, already malnourished (many deer herds in the United States), but can hardly apply where the malnutrition and subsequent vulnerability cannot be attributed to a chronic shortage of food but instead is occasioned by temporary "crisis periods" during adverse weather.

During the occasional very severe storm when temperatures are well below zero and snow or sleet is accompanied by high winds, upland game birds and sometimes other animals may die from exposure even though in good flesh and with food in their stomachs. Those birds which survive are so weakened by the period of exposure that they may remain easy prey for several days or longer following the cessation of the storm. Immature bobwhites, ringnecked pheasants, wild turkeys, and other game birds may be temporarily enfeebled by cold rains and be easily caught by almost any predator.

The taking of diseased or injured animals by predators is called the "sanitation effect" by some writers. There appears little reason to doubt the value of this service, and it may be exceedingly important in the survival of some species. By eliminating the weak, the diseased, and the crippled before they can breed, physical degeneration is inhibited. This "survival of the fittest" may contribute to the evolution of a hardier, wilder, more sporting game animal.

Latham and Studholme (1947) have advanced the hypothesis that the importation of bobwhite quail from southern states and Mexico into certain northern states has created a hybrid bobwhite which is unsuited to the rigorous climate of that region. Because during two different severe winters (1935-36 and 1943-44) more than 90 per cent of the resident bobwhite population was lost in Pennsylvania, and because during most winters the mortality from the combined forces of malnutrition, exposure, and predation is high, it is reasonable to assume that much of this susceptibility to predation may arise from genetic weaknesses especially when it is known that losses prior to the period of importation were comparatively negligible.

Yeatter (1934) describes "mudballing," or "clayballing" as it is known in Europe, as a cause of mortality among Hungarian partridge chicks. Ducks which swim into oil films on the water become helpless. These and similar mechanical handicaps add to the availability of prey animals.

(d) *Amount of protective cover provided by habitat.* With few exceptions, small game, or small birds or mammals of nearly any kind, will not thrive where there is a sparsity of vegetative cover even though food may be adequate. Quite often the numbers of the prey population ar directly proportional to the amount of protective cover, with predation appearing to be the controlling factor.

The sparsity of cover upon land may be fairly constant as upon badly eroded areas; it may be seasonal as the reduction which follows fall frosts; it may be temporary as that which follows plowing or forest and prairie fires, or as caused by heavy snows. Whatever the cause of reduction, a sudden or gradual loss of

cover invariably means an increased vulnerability of small prey animals and a reduced carrying capacity of the land.

Errington (1934) observes: "Cover is of value to the bob-white chiefly as protection or concealment in case of attack by enemies. Lack of cover means vulnerability to predation, whether enemies are few or many. Cover also has a certain value as shelter during periods of wet or cold weather, or during storms, but the necessity of shelter for the bob-white is usually overrated about as much as escape cover is underrated."

(e) *Introduced species.* It is obvious that exotics cannot be represented in the diet of a predator before introduction. Therefore, food habits figures for a predator may change considerably after one or more new prey species have been introduced and have prospered. In recent years the ringnecked pheasant has become an important food item of the fox in certain areas and the Cooper's hawk-starling relationship is well known. The barn owl, which normally feeds almost entirely upon small mammals, will take English sparrows and starlings because of their easy availability when roosting in barns and other buildings accessible to both predator and prey.

Following the introduction of exotic game animals, there is often a regular stocking of pen-reared birds or mammals from game farms. Most often these artificially propagated animals lack the psychological qualities so necessary for survival in the wild. Because these traits for self-preservation are undeveloped, mortality from predation is especially severe during the first few days or weeks after liberation. Newly released birds are sometimes killed by hawks on their initial flight from the shipping crate. This destruction of game-farm stock will be discussed more fully in a later portion of the report.

(2) *Density of predator population.* "The relative numbers in which a species occurs greatly influence its ecologic and economic relationships. A rare species or one present only in few numbers in a given region may be of little biological importance, even if its activities are in general detrimental to the best interests of certain other species or to agriculture or forestry. But an over-abundant species, even if it might be beneficial when present in moderate numbers, may, by reason of its overabundance, be forced to use plants or animals for food which ordinarily it would ignore, and it may thus become a devastating pest. The abundance of a species may therefore determine whether or not it is detrimental and in need of control, or of negligible importance. Information secured from a survey of a region made in one year may not give a true picture of the ecology in a subsequent year, because the relative abundance of all the species concerned will very likely have changed in the intervening time." (Dice, 1938)

Leopold (1931) states that "broadly speaking, therefore, variations in the damage inflicted by predators upon game must arise largely from local variations in the density of predator populations and from differences in food habits of the various species."

In his discussion of fox-quail ratios in different counties of Missouri, he continues: "It is easy to see how one fox per 75 quail might result in serious depredations, whereas one fox per 1,500 quail could hardly be felt, no matter how strong the disposition to catch quail.

"It is such evidence as this that forms the basis for my opinion that the fox question is not so much one of whether foxes do more harm than good, but rather a question of what density of fox population affords the best balance between harm and good."

Predator-prey ratios are sometimes surprisingly unbalanced. During the recent irruption of foxes in Pennsylvania, which reached a peak in 1946 when 47,664 red and gray foxes were submitted for bounty, the ratios between foxes killed and game killed by hunters demonstrated the superabundance of these predators. During that year, six foxes were killed for each quail shot; 20 foxes for each wild turkey; a little more than one fox for each grouse (1945, closed in 1946); one fox for each four ringnecked pheasants; and one fox for each thirty cottontail rabbits. When one considers that only a few thousand hunters and trappers actively chase or trap for foxes as compared to the army of well over 800,000 hunters who pursue small game in Pennsylvania, the possible destructive capabilities of the predator population becomes even more obvious. For the entire habitable land area of the state, it was estimated that there was one fox for each 125 acres in 1946, and in some regions the known density reached a high of one fox for each 12 acres.

The densities of emigratory species may fluctuate with startling abruptness. During the biennium 1935-1937, 1,781 goshawks were bountied in Pennsylvania, but, during a seventeen-year period (six years preceding 1935 and eleven years following 1937), only an average of 65 of these hawks were presented each year. The total effect of these hawks upon game populations during years of peak emigration following the "crash" of the snowshoe hare populations in Canada is tremendous compared to more normal years when as few as 15 have been bountied for the entire state.

The density of all other predator populations may fluctuate from year to year or from season to season. What is the significance of predator density to the proper interpretation of food habits tables? No matter how destructive a predator may appear from an examination of its diet, its total effect upon desirable prey populations is likely to be proportional to the density of the predator population unless the prey species itself is exceedingly rare and in danger of extermination, or unless the individual prey animal has a high personal-property value, i.e., livestock and poultry. In other words, could the 15 goshawks presented for bounty during the fiscal year 1942-43 in Pennsylvania materially affect the total numbers of ruffed grouse in the state even though each one is reputed to kill as many as 50 grouse in a single winter (Criddle, 1930)? Would 750 grouse, more or less, be noticeable in a population numbering into several hundreds of thousands? On the other hand, the 1,080 bountied during 1936-37 could kill, at the above rate, 54,000 grouse during the winter, and this number might have some significance in management. If the goshawks increased to 10,000 or 20,000, the resulting depredations might seriously reduce the numbers of grouse and cause acute shortages in certain areas.

(3) *Past and present predator-prey relationships.* Another variable modifying the interpretation of predator food habits tables concerns the past degree of control, or reduction, effecuated by a predatory species as related to its present association with the prey animal. It is conceivable that a predator population, because of an increase of numbers or because of fortuitous environmental changes, may be able to reduce markedly the numbers of a certain prey species over a period of a few months or years, and thus control this species at a low population level for an additional period of months or years. If food habits studies of the predator were made during the initial phase of the reduction period, the prey animal is likely to appear to be an important item of the diet and much

significance could be attached to the predator-prey relationship during this time. Later, after the prey population has been decimated and is being controlled at a much lower level, food sample analyses would reveal comparatively few of these animals in the diet. The tendency then, with no ecological information for guidance, would be for the interpreter to assume that the relationship was far more benign. However, the total impact of the predation is as great in the second case as in the first, even though the percentage of occurrence may vary considerably at the different times.

As would be expected, an almost complete reversal of the relationships defined in the above example would be possible under different conditions. A prey species may constitute the principal item of a predator's diet and yet be increasing at a rapid rate. This is often true of rodent populations.

(4) *Abundance or scarcity of buffers.* Many of the so-called "buffer" species, most of which are rodents, are cyclic in nature. These small animals which often partially divert the depredations of predators from game species, are likely to fluctuate, often extraordinarily, in numbers from one year to another. When a buffer species is at its peak of abundance, the diet of some predators may be largely composed of these animals, and, as a consequence, game and livestock may be relatively secure. On the other hand, when buffers become scarce greater pressure is thrown upon other species and the economic classification of a predator may change considerably. It is necessary, then, to ascertain the presence and relative abundance of buffer species before predator food habits tables can be interpreted with a reasonable degree of accuracy.

The value of buffers in the ecology of desirable wildlife will be discussed in Part II of this report.

Economic Classification of Predators

IT HAS been stressed again and again in this report that the economic status of most predators cannot be determined with any degree of accuracy from the interpretation of food habits tables without additional ecological information as a guide. There appear to be exceptions to this rule where the predator's diet seems to be almost wholly beneficial or wholly harmful. For instance, barn owl food habits studies almost invariably reveal a preponderance of small rodents, particularly mice, and few persons could deny the good accomplished by this raptor. However, it could be possible on non-agricultural areas that an abundance of barn owls would so seriously cut into the supply of mice that certain valuable furbearers could not thrive, and an important economic loss could be incurred by residents of the region. Goshawks, which are recognized to be exceedingly destructive to game, poultry, and other beneficial species may, on more primitive areas, be a significant factor in the survival of certain prey species. Particularly in cyclic animals, the removal of diseased individuals may greatly alleviate the devastating effects of the "crash" and prevent a species from sinking below a recovery level. All predator food habits tables, no matter how seemingly cut and dried, should have the careful scrutiny of a trained ecologist and an investigation of the ecological relationships upon the area involved before final judgment is pronounced one way or another upon a predator.

It is taken for granted that no "rule of thumb" method can be used

to classify a predator, but Dixon (1925) has suggested a guide to the evaluation of furbearers. He enumerates the credit and debit qualities of these carnivores as follows:

Credit

1. Value of pelts produced
2. Harmful rodents destroyed
3. Injurious insects eaten
4. Recreational value

Debit

1. Destruction of game
2. Destruction of domestic animals
3. Transmission of disease

Bennitt and Nagel (1937) propose a series of excellent questions which should be asked in the economic classification of any predator:

"(a) Does the *individual* predator destroy *only* members of the prey species considered?

(b) Do *all* members of the predator species destroy *only* members of the prey species considered?

(c) Do they kill active, healthy individuals, or do they cull out the weak, the diseased, and the crippled?

(d) Would the predator kill the particular prey if there were anything else available as a 'buffer'?

(e) Would the predator kill this particular prey if the latter had adequate cover?

(f) Does the predator compensate by killing other species injurious to man's interests or to the interests of the 'desirable' species?

(g) What would be the results of complete extermination of the predator?"

They also suggest that "from the human standpoint, no species is either wholly 'good' or wholly 'bad.' "

And McAtee (1931) warns that: "What needs to be kept in mind at all times is that in assigning economic values to natural enemies, it is best to speak in terms of tendencies rather than of achievements. Good economic tendencies are as satisfactory as any grounds for advocating the protection of natural enemies."

The intricacy of the problem is illustrated by Snyder (1947): "If we assume that man's interests are paramount—that we have the prerogative to condemn or acquit other creatures that live according to natural law, and that there are no extenuations even though the predator is virtually 'baited' to the farm yard by unprotected poultry—there is still great difficulty in establishing a full and fair economic evaluation on a hawk or an owl. For example, it is an established fact, and well known, that meadow mice girdle and destroy young orchard trees and that deer mice consume and foul cereal grains. This booklet, and many other similar studies, establishes the fact that several species of owls and certain hawks destroy these mice regularly and in quantity. If we search no further for facts we can regard these birds of prey as strictly beneficial. But if our economic accounting is more complete and thorough we will find that the food animals—mice—are assets in some respects. Mice are important staple foods of valuable furbearing animals, and they destroy weed seeds and noxious insects. Of course, we must decide what is a weed and what is a noxious insect! Thus, the book-keeping of economic evaluation becomes more and more complex. For the most part, a study of the food habits of a certain bird can produce quantitative information, but precise and complete economic evaluation is impossible. If we must judge rather than measure, then the writer suggests that we can more adequately judge as to the desirability or undesirability of an individual bird at a given time and place than we can for a species throughout the year or over its whole range.

"It should not be overlooked that there are real values in wildlife which

are not economic and which cannot be measured quantitatively. Most people would admit that the familiar robin has a value but if evaluation is based on its food habits alone, it cannot be graded high. Robins raid the cherry orchards; they consume earthworms in quantity—these creatures are important in mixing and fertilizing the soil and in making it pervious to air and water. Do we not value the robin most for its song, for its moderate and flattering familiarity, for its very being? How can these things be given economic and quantitative values? How many songs equal a quart of cherries? What is the dollars-and-cents value of the sight of a soaring eagle, or the wise look of an owl?"

The interests of the people as a whole, and not the selfish desires of individuals or groups, should be paramount in evaluating a predator. "In determining the economic status of any species in a given region, it is necessary to know not only its ecologic relations to its habitat, to its food, and to its animal associates, but also it is necessary to know the relations of the species to the welfare of various groups of people in the community. In a farming community the interests of the farmers must receive careful consideration, but the interests of trappers, hunters, nature lovers, teachers, and scientists must not be neglected." (Dice, 1938)

Finally, the whole complex matter of economic classification of predators is summarized by Kalmbach (1934): "From the foregoing one comes to the conclusion that the solution of our more important problems in economic ornithology depends largely on exact and pertinent field observations, without which much of our stomach examination data would have little significance. More than ever in these days of local adjustments in problems of wildlife there is need for a correct interpretation of facts. To be able to identify items with specific exactness, items of utmost importance in the economic relations of the bird, and yet be unable to state whether those items should be placed in credit, debit, or neutral categories with respect to the economy of man plainly indicates that other methods of approach must at times be involved. By all means there must be no slackening in laboratory research, but wherever it is evident that this method is incapable of accomplishing the object sought, there should be no hesitancy in adopting also some other plan that will give corroborative or other evidence of the status of the species."

He continues: "Workers in economic ornithology freely admit that food percentages, however computed, still must be interpreted by the investigator before decision on the status of a species may be determined. Abstract decimal or fractional values cannot be subjected to mathematical formulae and results computed therefrom as can be done in problems of engineering or chemistry. One estimated percentage indicating a beneficial activity cannot be construed as offsetting an equivalent designation of opposite economic significance. After all the painstaking examination and computation of food percentages of a species have been completed, what we have is simply a somewhat more tangible and understandable picture of food preferences. The conversion of this into terms of human economics is a matter resting largely on the personal judgment of the investigator. The wider his field experience and the sounder his logic, the more accurate will be his appraisal. A sympathetic understanding of agricultural problems will add much to the value of his decision. Yet, at best, in the attempt to convert abstract food percentages into terms of human economics, the ornithologist still is confronted with a problem of no mean proportion or complexity."

WILDCAT

PART II

Predator Management

INTRODUCTION

THE predator problem must surely be as old as man himself. Perhaps, if there had been an abundance of red-shouldered hawks or roadrunners in the Garden of Eden, the serpent which caused the downfall of Adam and the subsequent tribulations of all his descendants might have perished before it could have accomplished its temptations.

Probably the first lowly forms of humanity exhibited some emotion akin to resentment as they peered from their caves at some large carnivore carrying off a highly prized food animal. And even worse than this unpleasant competition, *man during the earlier stages of evolution was an important prey animal himself.* Primitive man faced a real predator problem!

For countless centuries, predators had been ruthlessly destroyed at every opportunity and no single benefit was ever ascribed to their activities until ecologists and wildlife biologists of the past sixty to eighty years endeavored to separate the good from the bad and attempted to determine the true role of each living thing in the scheme of nature. However, this pioneer work has done little more than scratch the surface toward establishing the place of the predator in the economy of things. For this reason, controversy is at its height. A man may be right today and wrong tomorrow. A hypothesis accepted this year may be rejected the next.

The infancy of the subject and the serious need for much additional research can best be illustrated by the declaration that *almost any statement concerning predator-prey relationships or the over-all economics of any predator's activities can be wholly or partially refuted by scientific study, by direct observation, or by expert opinion.* Is it any wonder that predation and predator control are the most controversial subjects in wildlife management today?

THE UNIVERSAL LACK OF AGREEMENT ON THE PREDATOR QUESTION

Among the several groups which, because of selfish interests, prejudices, or other reasons, have taken firm stands concerning predation and predator control, there can be listed the sportsmen who resent the competition of predators for game or fish; the farmers and stockmen whose cattle, sheep, or poultry losses are a direct economic liability; the nature lovers who believe in the preservation and protection of nearly all animal species, predatory or otherwise; the game manager whose job is to provide the greatest possible number of a few chosen species for recreation, even if it is necessary to sacrifice the lives of predators to accomplish this end; the ecologist who alone looks at all possible effects of predation, beneficial and harmful, and attempts to establish the economic status of each species from this broad, unbiased viewpoint; and, finally, the indiffer-

ent group who, because they never hunt, fish, raise livestock, nor commune with nature, care little, one way or another, whether predators are killed or are not killed. Peculiarly enough, the indifferent group is probably larger than any of the others.

"No topic in the wildlife field is more controversial than that of predator relationships, and on none perhaps is there more loose thought and positive opinion based upon insufficient consideration of the evidence that is available.

"Individuals interested in certain forms of wildlife also may become partisan and prejudiced in their judgment and deprecate the faults and glorify the virtues of favored forms. The extreme views among sportsmen, conservationists, and even biologists, on the subject of predator relationships, without a full weighing of the evidence, add to the vast problem of the interrelationships of all living forms. This relationship cannot be comprehended either by citing isolated individual experiences or by purely theoretical biological thinking." (Gabrielson, 1941)

Dr. Gabrielson's final statement—*"This relationship cannot be comprehended either by citing isolated individual experiences or by purely theoretical biological thinking"*—is a warning which should be heeded by all persons who have taken a determined stand on the question, no matter what this stand may be.

Kalmbach and Linduska (1948) state: "We probably wil never see the day when there will be an unanimity of opinion with respect to the degree of control (we could more intelligently use the term management) that is most desirable for certain forms of wildlife. It will vary with every local situation, it will change with every season, and it will appear different from the viewpoint of every person in the same community depending on their divergent interests. The overall problem has much in common with that of managing forest lands and other public domain to obtain the greatest good for the greatest number and not, necessarily, for the total satisfaction of any one interest, however significant it may appear to be."

McAtee (1932): "The outstanding feature of correspondence that comes across the desk of the economic ornithologist is the whole-souled sincerity of the writers. To each of these, apparently, the individual point of view is so engrossing as practically to exclude all others, and so undeniably right as automatically to overwhelm any possible conflicting idea.

"Naturally, each correspondent expects sympathetic response, if not full surrender, to his argument, and that is one of the things that makes 'the first hundred years the hardest' for the economic biologist."

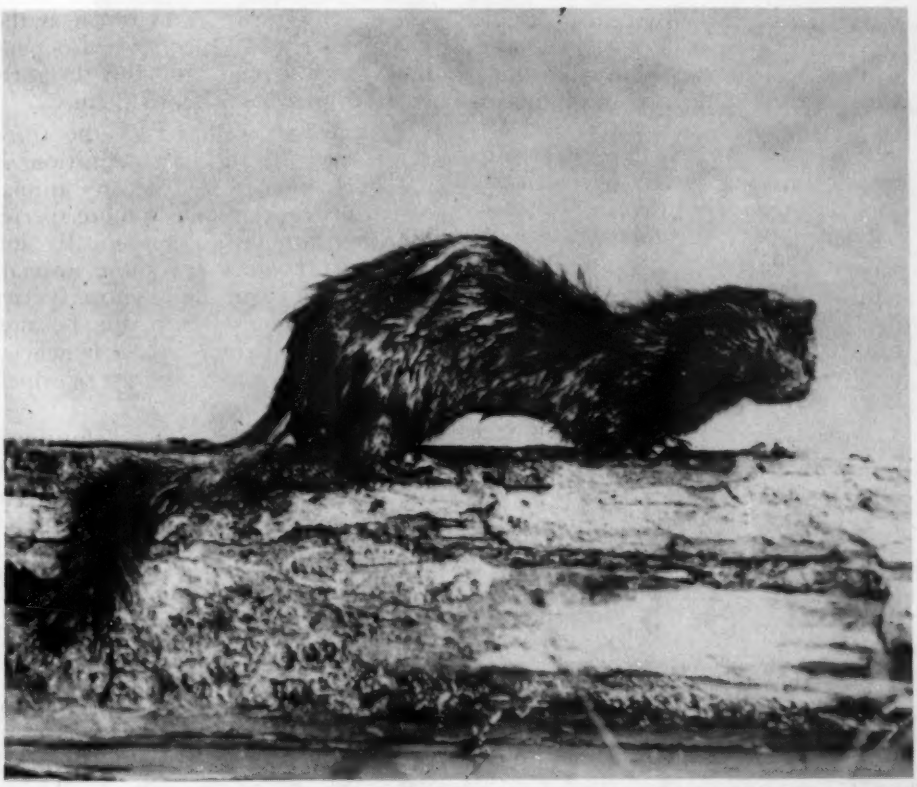
The ways in which conflicting groups may regard each other's thinking is described by Taverner (1939): "One group argues vehemently that every creature saved from the claws and jaws of natural raptors is one more that can be devoted to man's use or to the prosperity of the favored species. The other postulates that the predator is a normal and necessary factor in the economy of nature and its elimination would be disastrous to the end in view. The school that regards itself as being 'common sense' and 'practical' views its opponent as doctrinaire, theoretical and sentimental; the other school prides itself on its scientific caution, its wider field of vision and more exact knowledge of biological reaction."

Individuals and groups when confronted with facts, or when imbued with a greater knowledge of animal interrelationships, may alter their convictions concerning predation. Cahalane (1939) has said: "Whether based on research or current belief, predator management has been greatly influenced by superficial ob-

servation, personal bias, exigencies of the occasion, and group pressures. Control methods have varied, tending of late decades toward those of greater selectivity. Even the species included in official lists of predators have varied. Numerous at first, these became fewer with the passing years particularly by exclusion of the smaller carnivores."

Gabrielson (1941) reflects the possibility of changing opinion even among wildlife biologists when he says: "After fifteen years spent in intensive work in predator- and rodent-control problems and on studies of the interrelationships of predatory and other forms, the writer confesses that he is much less certain as to the significance of these relationships than he was before his biological theories had been tested by stubborn facts encountered in field experience."

It is significant that many of the men who have had the greatest amount of field experience—those who have studied the relationships between predators and their prey on the land—favor the control of predatory animals. Those who are vehemently opposed to predator control are often persons with little actual field experience in respect to this problem. In fact, many of the "protectionists" have never lived outside of a large city, and it is interesting to contemplate whether their attitude toward predators might change if they were to become farmers, ranchers, or even hunters for a few years.



PGC Photo by Latham

Predators, like the mink above, provide a valuable source of income to the trapper and hunter.

"A fully informed public will give scant attention to the opinions of Slingshot and Spittoon Clubs that loudly favor wholesale extermination of all 'vermin,' or the maudlin sentimentalities of Pee-wit Twitter Societies that flutter to the support of a 'hands off' policy toward all wildlife. A fully informed public will recognize the worth of predator and rodent control policies based primarily upon the economic necessities of resource conservation, except for predominance of esthetic considerations on specialized recreational, wilderness, and sanctuary areas. . . ." (Presnall, 1949)

Darrow (1947) and Grange (1949) both point out that one of the principal stumbling blocks in the way of agreement upon the predator question is the failure to differentiate between the fate of populations and that of individuals. Grange suggests that Nature is careless or indifferent to the fate of *individuals* but in the end careful and concerned with the fate of *populations* or *species*. Most of those who favor predator control are thinking in terms of individual animals lost, while most of those who oppose control are usually thinking only in terms of species or population survival.

WHAT IS A PREDATOR?

Webster's New International dictionary defines predator as "one who or that which is predatory." Predatory, in turn is defined: "(a) Living by preying upon other animals; predaceous. (b) Destructive; damaging (crops, buildings, etc.) by consumption; as *predatory* insects or birds."

Riter (1941) suggests a more restricted definition: ". . . a predator may be defined as any wild animal that preys upon one or more species of other wild animals that are being fostered in wildlife management plans."

Pearson (1933) perhaps gives the most poignant definition of all: "Vermin is any wild creature that kills something you want to kill."

Of course, either of these two definitions must be somewhat altered to be truly applicable. Riter by using the modifying adjective "wild" has excluded the domestic dog and cat in his definition, but these two animals are considered important predators in wildlife management. Pearson excludes prey animals which provide us with pleasures or benefits other than those derived from hunting or fishing. Some may, and do, resent the killing of a cardinal, as much as the killing of a game bird, by a Cooper's hawk, if the sight of this brightly colored bird has pleased them.

Perhaps a composite of the three would provide the best definition. A predator, then, would be any animal which preys upon one or more species of other animals. Economically important predators are those animals which prey upon one or more species of other animals which are, because of their activities, either beneficial or harmful to man's interest or which have esthetic value.

According to the above definitions, nearly any animal may, at times, be predatory. The titles of short notes from the *Auk* indicate the extent of predation. Here are a few picked at random: Purple Gallinule Robs Nest of Green Heron; Great Blue Heron Swallows Large Snake; Predation on Living Prey by the Black Vulture; Red-bellied Snake in Ruffed Grouse Crop; Black Vultures Kill Young Pigs in Kentucky; Golden Eagle Captures Red-shouldered Hawk; Leopard Frogs Devouring Small Birds; White-winged Junco Killed by Clark's Nutcracker; Hummingbird Killed by

Praying Mantis; Purple Grackle Kills English Sparrow; Coot Attacks Young Duck; and Red-breasted Merganser Devoured by Angler Fish.

The word "predator" to many means only animals of a harmful or destructive nature. But to the contrary, some of our most beneficial species are true predators. In the study of predators, one fact stands out above all others and that is *that the most destructive predators may under certain conditions be decidedly beneficial and those recognized as beneficial may at times or in certain places be definitely destructive.* And further, there may be predator-prey relationships as yet undiscovered which may be more deleterious to man's interests than many which are causing him grave concern at the present.

So, whether we call them predators, carnivores, natural enemies, vermin, or some other appellation, it should be remembered that these terms do not necessarily denote harmful activities, but that in many instances these specialized animals are among the most beneficial and most desirable of all forms in terms of human economy.

THE ECOLOGY OF PREDATION

The Role of the Predator in the Scheme of Nature

A fitting introduction to this portion of the report is given by Snyder (1947). He says in part: "To understand the place which birds of prey [or all predators] occupy in nature one must appreciate certain of the interdependences of different forms of life. Everyone is familiar with the fact that certain animals prey on smaller and weaker ones, but it is perhaps not so generally realized that this same principle is of universal application. The wolf eats the deer that browses on forest herbage; the lion devours the antelope that feeds on the grass of the African veldt; the fisher kills the porcupine that gnaws the bark of trees; the lynx lives on hares that feed, like the corresponding animals in the examples just cited, on vegetable matter. These are examples of food chains which are of universal occurrence in nature. But food chains frequently have more links than are shown by the examples given. For instance, the trout devours the minnows which eat aquatic insects; these feed upon still smaller creatures which in turn eat microscopic plants in the water. Although this food chain is longer than the others, it resembles them in two respects—the ultimate food material is plant matter, and the animal at the upper end of the chain is a carnivore.

"It will be readily appreciated that the numbers of individual animals in what may be termed the 'prey group,' must ordinarily be greatly in excess of the numbers in the group feeding upon them. Where there are a series of groups depending one upon the other for subsistence there is a tremendous expansion of numbers from the larger to the lesser—from top to bottom. . . . From the bottom to the top of the pyramid the creatures increase in size but decrease in numbers. The rate of increase of the different species which is determined by their reproductive capacities as modified by the percentage of survival among the young is ordinarily so balanced in nature as to maintain this pyramid of numbers.

"It has been pointed out above that the birds of prey, in common with other carnivores, occupy a very definite and pre-eminent position in the scheme of nature and we are led to speculate as to the role which the carnivore plays in such a scheme. To

understand this role we must remind ourselves of certain facts with reference to the numbers of living creatures. It is well known that most birds, mammals, insects, and other forms of life tend to increase very rapidly in numbers. For examples, mice have several young at a litter and usually several litters a year. Birds do not reproduce so rapidly, but if all the young which are hatched reached maturity and reproduced in their turn, the earth would soon be congested with birds. What actually happens under normal conditions is that the numerical abundance of birds, insects and other creatures remains moderately uniform. From a single pair of parents of a species maintaining a level of numbers, only two offspring, *on the average*, reach maturity and reproduce in their turn; all of the others perish. The principal factors which tend to level off populations are storms and severe weather, carnivores, parasites, disease and accidents. If it were not for the persistent action of these destructive forces each species would go on increasing until ultimately it had eaten all available food, resulting in death by starvation. Various species of insects from time to time break away from the control of natural enemies and multiply at an alarming rate. They sometimes denude trees of their leaves and devastate field crops over wide areas but ultimately a depletion of food results in their starvation, or so reduces their vitality that they perish from disease or disorders closely akin to disease. Another example of the attainment of extraordinary numbers is afforded by the varying hares of the north woods. Periodically the hares become very numerous and then some malady spreads among them and reduces their numbers almost to the vanishing point.

"Throughout the ages, by a kind of trial and error process, nature has evolved a safe and steady counterforce which works against the suicidal expansion that is potential in all species. An important factor in this counterforce is the carnivore. Birds of prey, for example, are a much safer means of controlling numbers than starvation or disease because there is always the danger that these scourges may wipe out a species entirely. Carnivores do not exterminate the species on which they prey. If their prey becomes very scarce they too cease to flourish since they cannot exist in numbers disproportionate to their food. Man is the only predator at all likely to exterminate a species."

Generalizations Concerning Predator-Prey Relationships

Gabrielson (1941) has outlined several basic principles of predator relationships:

"(1) Under normally stabilized conditions over a wide range, predators generally live upon surplus populations of prey species and their activities in the aggregate have little or no effect upon the breeding stock needed for the succeeding season. Local readjustments in accordance with varying conditions are often desirable to maintain a balance, though this can never be perfect; the observed *average* stability of animal populations emphasizes this point.

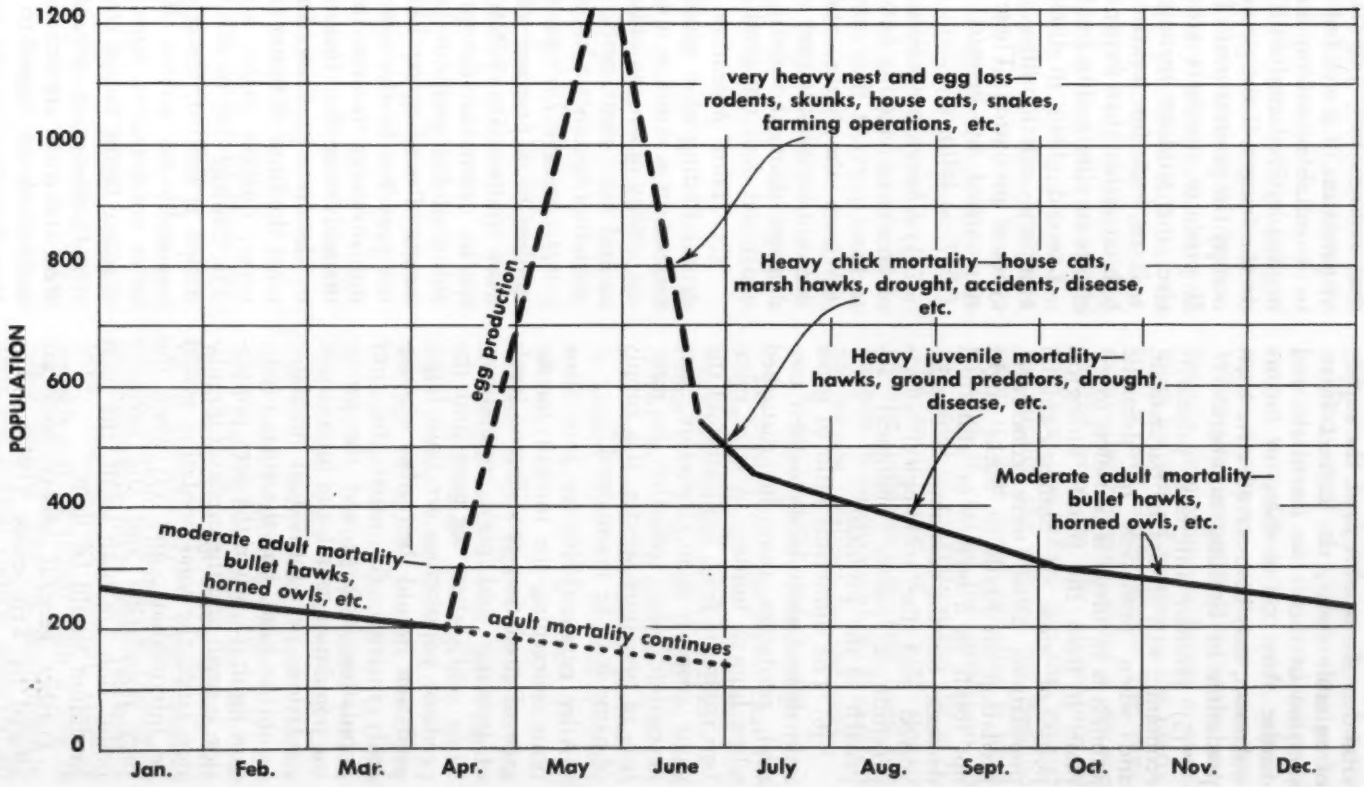
"(2) Under special conditions, either favorable to the predator or unfavorable to the prey, predators may become a real factor in decreasing populations or in preventing recovery following a decline in population.

"(3) The effect of predation upon population is more evident when the predator is a more prolific species than the prey. Where the reverse is true, the effect is at least obscured by the fact that the victim has a greater reproductive capacity than the predator.

"(4) Generally the agency of predators in reducing large populations

FIGURE 1

Diagram of the annual rise and fall in a population of valley quail and some factors that influence the seasonal changes in numbers. The population figures are approximate for a section of land, 640 acres. (From Emlen and Glading, 1945.)



is minor compared with the more vital one of available food, the supply of suitable cover, the correct interspersion of these two essentials, and disease. Any one of these, or factors unknown, may be more effective than predation in limiting numbers.

"(5) Human interests, primarily economic, will always be paramount, and when predation on domestic animals is involved it is useless to explain it from the purely biological point of view. If domestic-animal populations alone were concerned, predation on herds or flocks might not result in a serious or abnormal decrease, but the economic factors involved and the sociological effects preclude a purely biological approach to the problem.

"(6) The numerical ratio of game animals and game birds to their natural predators may be disturbed when human hunters in large numbers enter the field. Utilization of the game crop by man, therefore, may necessitate some reduction in numbers of predatory species, if a supply of game is to be maintained."

Allee et al. (1949) list generalizations concerning the intensity or degree of predation at different levels of predator and prey populations: ". . . (1) when the prey and the predator populations are both large, predation would be rather consistently intense; (2) when the prey population is large and the predator population small, the intensity of predation per individual predator would be high, but the total predation light; (3) when the prey population is small and the predator population large, the total predation would be intermediate; and (4) when the prey population and the predator population are both small, the total predation would be light."

Further general observations are offered by Trippensee (1948): "The effects of predation on a prey species as indicated by a variety of studies might be stated as follows; Predation is only one of the forces of nature that reduces prey populations. Loss by predators of a well-fed population in a suitable environment will be negligible. Predation will be heaviest on the fringes of the population that occupy the poorest part of the range. If predator numbers are not excessive, the wildlife manager will do well to look for weaknesses of the habitat rather than expending undue efforts in eliminating predators."

Leopold (1933) in discussing predator-prey relationships listed five types of predation. These have been summarized by Bennitt and Nagel (1937) as follows:

"(1) *Chance predation.* The result of accidental meeting between predator and prey. It does not select the 'fit' from the 'unfit' and therefore does not benefit the prey species. The damage done, however, is usually small and does not tend to increase.

"(2) *Habit predation.* The accidental finding of a quail nest by a raccoon or a skunk is apt to develop the ability of an *individual* predator to find more nests, until this type of predation becomes a habit.

"(3) *'Sucker list' predation.* The capture by a predator of a few unwary individuals, before the prey species learns of the presence and habits of the predator and develops means of evading it. The benefit to the prey lies in the 'education' that the survivors receive in protecting themselves against future onsloughts by the same predator. In quail, this takes the form of better use of escape cover, quicker flight, and the like. The damage due to this type of predation is limited, though it may occasionally be serious if food and cover are deficient, especially if food is scarce in the escape coverts.

"(4) *Starvation predation.* Where food and cover are deficient, the prey individuals are forced to an unaccustomed degree into the open to avoid starvation during bad wather. Starvation predation is to some degree

selective, in that the hardier individuals are likely to be the ones which survive longest. . . . Consequently, this type of predation is beneficial unless it annihilates a large part of the prey population, because it weeds out some of the weaker individuals.

"(5) *Sanitary predation.* In this type also, the predators cull out the 'unfit'—i.e., the crippled, diseased, slow, or stupid individuals. The damage is small, and the benefit to the prey species is obvious. It is just what the breeder of domestic stock does when he culls out his flock or herd, retaining the superior individuals for breeding purposes."

A mathematical study of predator-prey relationships was introduced by Kelker (1939) and was proposed to illustrate the fact that one predatory species may control one prey species, even though the prey species is a faster breeder, and other conditions are equal.

His problem reads: "Given an early spring population of 10 badgers per square mile and 15 ground squirrels (*Citellus*) per acre; the badgers have one litter of 4 young per season, the *Citellus* have 2 litters of 4 young per litter; one badger kills 2 *Citelluses* per day for 120 days before the latter hibernates; and furthermore, assume that of the 240 squirrels killed, one-half are the spring breeding stock (hence are killed before they reproduce). What are their relative numbers at the end of 5 years? Assume no other losses for either animal. Sex ratio is always equal or 0.5.

Final Fall Population of Predator and Its Prey

Year	*First*	*Second*
Badger	30	90
Citellus	26,400	67,200
Year	*Third*	*Fourth*	*Fifth*
Badger ..	270	510	1,530
Citellus ..	141,600	124,800	None

"Under the actual field conditions, no predator will exterminate a given species of prey because the toll on it decreases as it is harder to find, until at a given low point practically all of the predator-pressure is turned to other foods, whereupon the prey starts to increase. When its numbers are again sufficently numerous to bring a minimum amount of success to the predator, it will again harass the prey, eventually bringing about a decline in the prey. So the abundance of the prey fluctuates, for the greater the supply, the greater the demand upon it. The above equation is weak in that it carries the predation to the point of exterminating the prey. The annihilation of a prey species by the predatory species does not happen in an environment that offers any escape facilities for the prey."

Inter-Predator Relationships

Leopold (1933) mentions that the steady increase in numbers of weasels bountied in Pennsylvania between 1915 and 1930 might be coincident with the reduction of hawks and owls over the same period. It is known that the horned owl for one is a potent predator of the weasel.

Later bounty figures for Pennsylvania suggest still another inter-predator relationship. During the eight-year period from 1932 to 1940, an average of 65,000 weasels were presented for bounty annually (a high of 89,000). During this same period, the kill of foxes, both red and gray, averaged somewhere near 15,000 each year. Beginning about 1940, the fox population irrupted and the numbers taken increased rapidly until by 1946-47, 47,000 were bountied in one season. During this eight-year period, while foxes were reaching a peak, the average annual take of weasels fell to 15,000 with a low of 5,000 during 1944-45. Significantly, after the partial control achieved by eliminating 47,000 foxes in 1946-47, over 21,000 weasels were presented

for bounty. Whether weasels continue to increase in numbers as the fox population decreases remains to be seen.

Besides weasels, foxes are known to kill skunks, opossums, red squirrels, Norway rats, crows and other mammalian and avian predators with some frequency. Horned owls commonly kill skunks, opossums, weasels, smaller owls, crows, hawks, Norway rats, housecats, minks, and others. In fact, hungry horned owls caged together will readily exhibit cannibalistic tendencies. Crows will eat the eggs of both hawks and owls, and red-tailed hawks are one of the foremost enemies of red squirrels.

With the extension of its range into Alask , the coyote has become a serious menace to the fur industry there. Goldman (1930) has this to say: "It is even possible to trace the advance of coyotes by a marked decrease in the fox population, and

Photo Penna. Game Comm.

Pennsylvania's four dollar bounty on foxes provides an added income for rural trappers.

the trappers note it with dismay, for they are thus deprived of a valuable source of revenue . . . In many cases a family or entire colony of foxes are run out of their dens or are both run out and killed by coyotes which then use the den themselves. Wolves are well known to have committed similar depredations, but their killing is not so extensive as is that of the coyote . . ."

Probably the reader can think of other cases of predator killing predator, for there are many more, but just a few have been mentioned to emphasize the fact that this relationship does exist.

Its importance in the ecological complex of living things has yet to be determined, but, where this inter-predator strife tends to reduce materially one species while another prospers, the resultant modification in animal interrelationships may be of considerable significance.

Inter-Prey Relationships Between Desirable Wildlife Forms

Under certain conditions, desirable prey animals which the wildlife manager wishes to protect against predators, may exhibit predatory tendencies themselves. For instance, Stoddard and Konmarek (1941) found: "Curiously, destruction of quail eggs and very young birds by heavy populations of wild turkeys may make it difficult to maintain high turkey and quail populations on the same ground, and owners may be forced either to discontinue quail shooting on lands where wild turkeys are becoming abundant or maintain a better 'balance' by bagging more of the turkeys."

Not too much is known concerning the inter-species relationships of prey animals—and especially of game animals. Leopold (1931) reports an instance of a cock pheasant killing an adult quail, but whether this occurs with sufficient frequency to warrant concern is a question still unanswered. There is a common belief, but without much supporting evidence, that pheasants kill and eat many immature cottontail rabbits before they leave the nest. Errington (1945) suggests that pheasants may deprive bobwhite quail of good winter cover, because of interspecific intolerance, and perhaps push the quail out into less choice sites where they become more vulnerable to predation.

At times, more indirect relationships, such as competition for food, the destruction of herbaceous cover, or the dissemination of diseases, may be far more important as limiting factors than the more direct interspecific strife just illustrated. The ill effects of over-browsing by deer upon populations of cottontail rabbits, ruffed grouse, varying hares, and other forest-dwelling small game species is well known. The spread of diseases to wild game birds by wide-ranging poultry flocks is also recognized.

Perhaps future studies will disclose even more important inter-prey relationships.

The Relation of "Buffer" Species To Game Predation

Like most subjects relating to predators or predation, there is not complete agreement upon the value of buffers in preventing predation upon game animals. At first glance, it would appear that large numbers of small rodents (mice, rats, ground squirrels, etc.) would satisfy the hunger of predators, and the game, where these small mammals were abundant, would be comparatively secure. However, Stoddard (1931) thinks differently: "The theory has frequently been advanced that such rodents act as 'buffers' between the upland game birds and their predatory enemies, and that if they were destroyed, the enemies of game birds would turn more to the quail or their eggs and do vastly more damage in conse-

Photo Penna. Game Comm.

Small rodents, such as mice, rats, red squirrels, gophers, etc. constitute a "buffer" for game.

quence. In some cases there may be a measure of truth in this contention, but in general our field observations indicate that the theory is unsound so far as Southern quail preserves are concerned. Here an abundance of the rats [cotton rats] attracts an abundance of enemies to prey upon them. Red 'chicken snakes' (red colubers) and other snakes, which prey upon rats regularly and quail eggs incidentally, are usually found in the most 'ratty' places, while the abundance of marsh hawks in any particular locality seems directly in proportion to the number of rats, or their availability. The same holds more or less true for skunks, homeless cats, and others.

"Hence if the quail preserves are kept as free of rats as possible many of the creatures that are attracted primarily by the rodents, but damage the quail incidentally, will consider the area poor hunting-ground and confine their efforts to places where the rats are abundant. This happy hunting-ground may well be on the lands of others outside the confines of the preserve."

Stoddard found that this particular buffer (the cotton rat) destroyed more quail eggs than any other predator in the South.

In speaking of the same region, Errington (1938) postulates: ". . . On the upgrade of their cycles, uncontrolled cotton rat population may become so numerous as to attract and perhaps build up locally populations of predators that destroy many quail incidentally. When the cotton rats rapidly decline under such conditions to the extent that they are no longer readily available as a staple food for certain types of predators, these predators, in turning to other sources of food, may seriously affect bobwhite populations . . ."

Komarek (1937) agrees with both Stoddard and Errington: "As Stoddard brought out in 1932, my studies indicate that a high population of small mammals is not necessarily a buffer against predators but conversely that such a population not only attracts but builds up a higher predator population. Food is considered by most game research men to be one of the main criteria for building up a game population; why not a predator population?"

And Darrow (1945) found ". . . Thus it seems that when a low abundance of buffers, their staple food supply, forced foxes to cover the area more intensively to get enough to eat they happened onto and destroyed a greater proportion of the grouse nests present."

The subject of buffers is nicely summarized by Leopold (1933): ". . . It is obvious that in the ag-

gregate they act as buffers to divert the attention of predators and satisfy their food requirements. This benefit is partially offset, however, by the fact that most of them compete with quail for food, while some of them (for instance, spermophiles) are themselves possibly predators on quail, in that they eat eggs and possibly chicks. There is still another possible offset to the beneficial effect of buffers: they may, provided they are more abundant than elsewhere, act as "bait' which induces an influx of mobile predators. Furthermore, some buffers harbor the diseases of game, and many the diseases of predators. Lastly, hibernating buffers are unavailable to most predators during the winter, and nocturnal buffers are not available to diurnal predators, or vice versa."

Similar to the effect of hibernation, high mouse populations, which may have attracted many predators, may become unavailable during periods of deep snow and thus throw the predator pressure normally absorbed by them onto small game which, because of the sparsity of protective cover, is at these times most vulnerable to predation.

Failure of buffer (perhaps a misnomer in this region) populations in the far North (snowshoe hares and lemmings) may: (1) cause the mass starvation of certain predators; (2) throw undue pressure upon grouse and ptarmigan; or (3) cause an emigration of predators to other regions. This is the principal cause of goshawk and snowy owl "invasions" into northern United States. When these invasions occur, the native game of these states may suffer abnormal losses. The high mortality of ruffed grouse to emigratory goshawks is well known.

The Effect of Prey Populations Upon Predator Populations

Since predators are primarily dependent upon prey animals for food and consequently for survival, any failure or scarcity of this supply is certain to produce much the same results as a similar scarcity of food would for herbivorous animals.

Such far northern predators as the Arctic fox, snowy owl, goshawk, and Canada lynx may suffer moderate to severe mortality when the "crash" of the lemming and snowshoe hare cycles coincide and the available food is reduced to almost nothing. This fact is substantiated by the records of the Hudson Bay Company. Because of their greater mobility, goshawks and snowy owls may emigrate southward until they reach a new food supply. In temperate climates where prey species are far more numerous, the temporary scarcity of a cyclic prey animal merely means a temporary diversion of its predators to one or more other prey species. Emigration may even occur, but the extent of this may be no more than a few hundred yards or a few miles as compared to the many hundreds often traversed by snowy owls and goshawks during food depressions.

Besides the possible starvation or forced migration of northern predators, there is another important way in which the supply of prey may affect predaceous animals— the physiological effect upon reproductive success. Gross (1947) explains this relationship: "It is now generally accepted that the underlying cause of Snowy Owl invasions is the well-known cyclic fluctuations in the lemming and mouse populations.

"The lemmings increase over a period of three to five years—an average of approximately four years —from a low ebb to a maximum. The year of maximum abundance of lemmings is also a good year for the predators. The Snowy Owl fits into the picture somewhat as follows. The owl lays from six to eight eggs, and some nests have been found to contain as many as thirteen. When

Photo by Hal Harrison

When the periodic shortage of prey animals occurs in the Arctic and Sub-Arctic, the snowy owl may emigrate as far south as northern United States.

the eggs hatch, it requires a tremendous amount of food to feed such a large family. Ordinarily the mortality is great, with only two or three of the owlets reaching maturity. If the lemmings are scarce, the owls may not even attempt to nest. In a good lemming year, practically all of the large families survive, and thus the snowy owl population is built up to a peak along with that of the lemming. The same might be said of the other predators. Then with abruptness the *'crash'* comes.

"The predators such as the foxes and the Snowy Owls that depend primarily upon lemmings for food must do one of two things—they either starve to death or they must find other sources of food. The foxes are able, by their cunning and adaptiveness, to secure other food, but many of them die of starvation and disease as the Hudson Bay records clearly indicate. The Snowy Owl, however, since it is able to fly, wanders far and wide, in years of extreme general scarcity of lemmings, even coming down as far as northern United States. It is clear that the migration of the owls is due to two factors: first, the great increase of the Snowy Owl population; and, second, the abrupt disappearance of their chief food, the lemmings.

"Other predators of the lemming also exhibit, though not in such a spectacular way as does the Snowy Owl, the influence of the lemming cycle. Gyrfalcons, Rough-legged Hawks, Short-eared Owls, Ravens, Shrikes, and others have usually been noted in increasing numbers during the times of the Snowy Owl invasions. The lemming cycle exerts a profound influence on the ecology of the Arctic barrens. It is not only the basic cause of periodic migrations of predatory birds, but it also vitally affects the furbearing animal and thus the whole economy of the Arctic fur industry."

Elton (1927 and 1942) has recorded other instances of food shortage limiting the reproduction of predatory animals: ". . . the short-eared owl (Asio flammeus) may have twice as many young in a brood and twice as many broods as usual, during a vole plague, when its food is extremely plentiful." And Manniche (1910) in writing of the mammals and birds of Greenland reported that skuas and snowy owls breed chiefly or solely during the lemming maximum.

A Comparison Between Predation and Other Factors Causing a reduction In Prey Populations

Of all the perplexing ramifications of the comprehensive subject under discussion, perhaps the relationship between predation and the other factors controlling the size of animal populations is the most complex and least understood of all. Why are some species exceedingly numerous and others extremely rare? How can one animal with a low reproductive capacity occur in large numbers while another on the same range and blessed with an almost unlimited fecundity is barely able to survive? What are the effective reducing factors for each population or population fragment? There are many of these controls, including predation, and the problem of deciding which one is most effective at a given time and for a given population is indeed a test of superior knowledge and wisdom. Our task here is to examine the meagre information available and attempt to appraise the relative importance of each of the several restrictive forces in terms of animal survival.

That these forces do exist and are constantly in operation is accepted fact, and according to Southern (1948): "It must quickly become clear, if one considers the enormous potential increase of any animal, not only that mortality on the same high

scale must be operating (which is important for the evolutionist studying the working of natural selection), but that the operation of this mortality must be extremely precise to keep a population relatively steady in numbers from year to year. If an animal which increases by 100 each year is reduced before its next breeding season by 99 instead of by 100, this small discrepancy will generate an astonishing increase in a few years."

But before beginning a discussion of population controlling factors, it might be well to clarify the meaning of "control" as here used. Nicholson (1933) has differentiated between decimating or reducing factors and true controlling factors: (from Southern, 1948) "Nicholson formulated clearly the idea that, while many mortality factors operated on a population, only those whose pressure automatically increased with increase in the size of the population could be said to be controlling that population. A hard winter will not kill animals in proportion to their total numbers, and, therefore, although more may die from this cause than from any other, it cannot be said to control them. Predation, on the other hand, will vary in intensity with the numbers of the prey and may be said to control them. In Nicholson's phrasing, predation is a density-dependent mortality factor. These factors can be classed in three broad categories—availability of food, disease, and predation (of which parasitism may be considered as a special form)—and all other kinds of mortality are density-independent and, as such, unable to control the animals upon which they act." The writer feels that *emigration* should be added to the list of density-dependent factors. Elton (1927) attests to the importance of this factor in population decrease.

Nicholson explains this hypothesis as follows: "We will suppose that the animals in a certain population would increase one hundredfold in each generation if unchecked, and also that, on the average, climate destroys 98 per cent of the animals. It is clear that the number of animals would be doubled in each successive generation if no other factors operated. Climate could never check this progressive increase, for it would continue to destroy only 98 per cent, its action being uninfluenced by the density of the animals. If, however, there is some other factor, such as a natural enemy, the action of which is governed by the density of animals, the destruction of the remaining 1 per cent, necessary to check an increase, would soon be accomplished. If this example were observed in nature, one would be tempted to conclude that, because climate destroys 98 per cent of the animals while the natural enemy destroys only 1 per cent, the limitation of the population is mainly due to the influence of the climate. However, it is clear that the natural enemy is wholly responsible for control, because climate, by itself, would permit the density of the population to become indefinitely great."

Southern (1948) shows that animal population levels may vary in accordance with the particular control factor operating: "Consideration of the work described above brings us to the conception that the steady density of any animal may vary not only with environmental changes (e.g. by a direct or indirect alteration in the searching efficiency of the predator, which may be controlling it), but may be set at widely-varying levels according to the particular control factor operating. An example of this is seen in the population changes which have been recorded for forest species of deer in America. Destruction of predators re-

sulted in the deer escaping completely from their control and multiplying enormously until they reached a new steady density in relation to their food supply—with disastrous economic repercussions. It is probable that many animals that show occasional 'mass increases,' whose economic importance is emphasized by the designation of plagues, have escaped from the control of predators or parasites and are reaching up to a new level set by the availability of food . . ."

The population levels as set by the four principal controlling factors—disease, emigration, predation, and food supply—can be shown graphically (Fig. 2). The levels shown, although of course varying widely in amplitude from the average or mean, may be applied to both cyclic and non-cyclic species, providing both exhibit irruptive tendencies and are subject to epidemic disease or mass emigration. A to B indicates the normal, expected increase of a population which has started at any low point; B to C is the more or less constant level corresponding reasonably close to Errington's "carrying capacity." Not always, but often, predation is the primary controlling factor at this level. Many so-called non-cyclic species may remain at this level for a number of years, with constant fluctuations above and below the line as fixed by weather and other density-independent factors. Many game species appear to occupy this level more or less permanently. C to D represents the "'irruptive" phase of population increase when, for some reason, a species may escape from the control of its natural enemies and reach a new level (D) set by the availability of food. Sometimes this escape may occur when the predator pressure is decreased, as in the example cited above of deer in America, or when the reproductive rate of the prey species, because of unusually favorable conditions, may suddenly greatly exceed the loss from predation. D to E marks the level set by the food supply, subject to the same variations in amplitude from density-independent factors. E to F denotes the "crash" phase which so regularly follows an irruption of numbers. In some species this may be terminated by disease, but in others, especially where plague proportions are reached, the "crash" may come as the result of mass emigrations. What initiates this decline is still somewhat obscure; sometimes the food supply is literally exhausted, and starvation, coupled with decreased reproduction, causes a decided slump; in other cases, epidemic diseases appear to strike when a certain population density is reached; and finally, emigration seems to occur more as the result of overcrowding than of a failure of the food supply.

It can be seen from the above discussion that predation, at least in most instances, occupies a median position between the food supply and disease (or emigration) as a population controlling factor. The food supply is ordinarily the least restrictive, predation is next, and disease (or emigration) causes the greatest reduction.

But if one does not differentiate between density-dependent and density-independent factors, predation becomes a far less important population-suppressing factor. Gabrielson (1941) says: "Every careful study that has been made of the relationship of predators and small-animal populations indicates that predation is not the major limiting factor upon the total populations of these species. In almost every case investigators have ranked predation as subordinate among suppressive agencies." And Nagel (1949): ". . . There's the fact (that we're just beginning to appreciate) that *when predation becomes the chief factor*

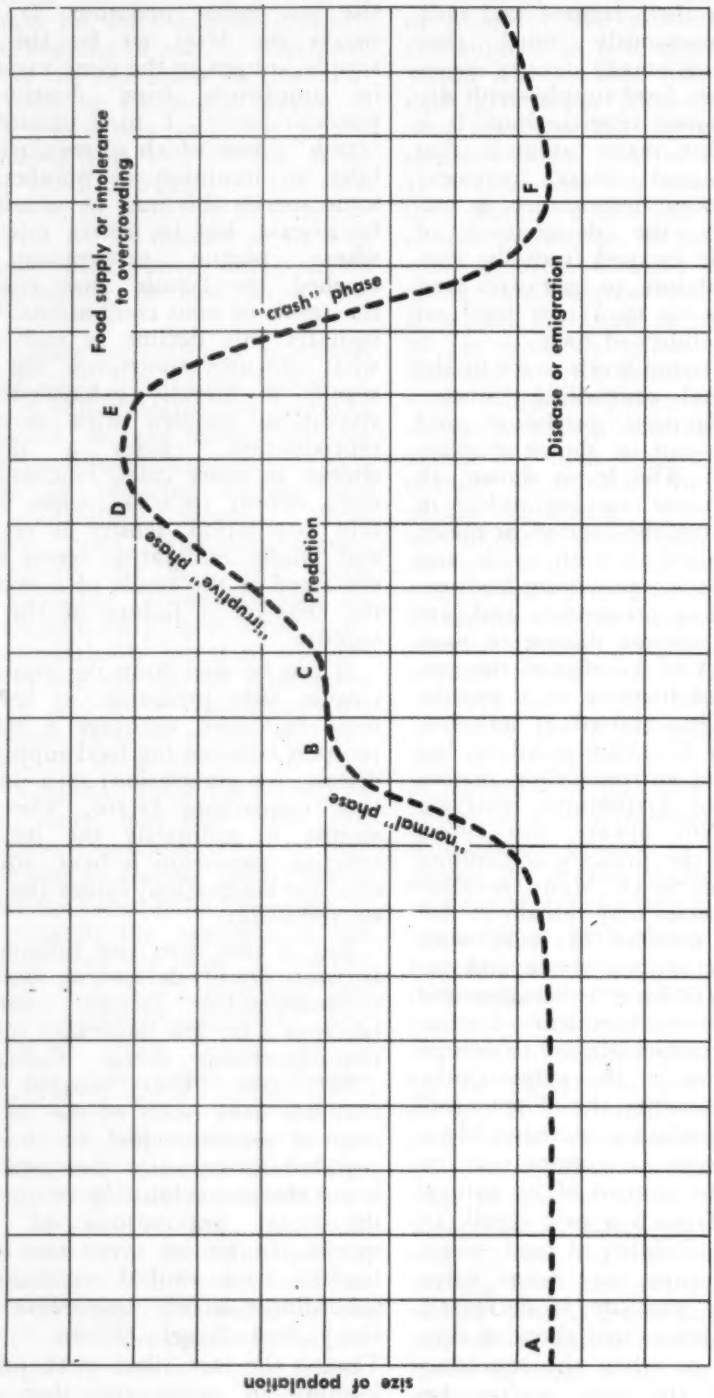


FIGURE 2

A Comparison Between Predation and Other Factors Controlling Prey Populations

in wiping out a game species, that species has outlived its environment."

Bennitt and Nagel (1937) have proposed two generalizations concerning predation and other controlling factors:

"(a) . . . decrease in predation is *not* accompanied by a corresponding increase in the prey species, except up to a certain point fixed by other factors such as food, cover, and breeding facilities.

"(b) . . . increase in predation is *not* accompanied by a corresponding decrease in the prey species, except down to a certain point fixed by the same factors."

Naturally, general statements like these are decidedly indefinite, because the difference between the population level set by predation and that fixed by any one of the other factors mentioned might be insignificant or it might be great. And again, the writer would like to stress that for most prey species, the population level fixed by *cover* is nearly identical to that set by predation.

Quantitative measurements of mortality from predation as compared to total mortality from all causes have been few in number. Tinbergen (1946) measured the mortality suffered by four species of small birds from the European sparrow hawk *(Accipiter nisus)* and compared this loss to the total expected mortality for each species. From the review of his work by Hartley (1947): "In the Hulshorst-Heiden area, where the figures are most complete, the expected total mortalities of House Sparrows in the months of May and August were 302 and between 678 and 833 birds. The deaths due to Sparrowhawks were 106 and 331, the latter figure being nearly 50 per cent of the lower limit of expected mortality. In the chaffinch in May the expected mortality was 170 birds, and 55 were known to have been killed by Sparrowhawks. In the two titmice the expected mortalities and the number of birds which fell to hawks are shown below:

	May	*June 16 Sept. 15*
Great Tit		
Expected	210	2,906
Killed by Sparrowhawks	93	529
Coal Tit		
Expected	357	5,569
Killed by Sparrowhawks	132	138

"On the basis of these data and of results from another sample area (Ermelo) it is concluded that the attacks of Sparrowhawks are the cause of at least half the summer mortality of House Sparrows; of about a quarter of the mortality of Chaffinches and Great Tits; and of only a small percentage of the deaths of Coal Tits."

THE ROLE OF THE PREDATOR IN WILDLIFE MANAGEMENT

Arguments Opposing Predator Control

(1) *The "balance of nature" concept.* One of the most widely-used arguments in opposition to predator control is that these animals are essential in maintaining a "balance of nature." The proponents of this concept insist that, without this balancing effect or counterforce, many injurious animal forms would increase at such a tremendous rate that the very existence of man would be jeopardized. Also, they contend that beneficial forms, unless held in check, would outgrow their food supply and eventually succumb by starvation. Thus, they visualize a harmony, a sanguinary relationship to be sure but harmonious nevertheless, among wild animals in which populations are maintained at a more or

less constant level. These levels are believed to be somewhere near the biological optimum for the various species.

What is the viewpoint of the ecologists on this subject? "The environmental changes wrought by civilized man are often much more rapid [than nature]. In a few decades we destroy vast forests, bring under cultivation thousands of square miles of prairie soil, carry water into arid regions for irrigation, drain great swamps and lakes; destroy immense herds of bison or other mammals, or myriads of pigeons, obliterate the hiding and nesting places of many species and reduce their food supply; introduce various other species, such as cattle, sheep, English sparrows, etc., to provide competition for native species of animals, and grains and other plants to provide competition with native plants and to furnish new, different and perhaps better food supplies for some of the native animals. In many other ways we disturb the balance that has been established. Such rapid transformations in the environment introduce many complex and difficult problems, the correct solution of which requires an accurate and comprehensive knowledge of all nature, and taxes the wisdom of the best-informed naturalists; yet men with very little knowledge of nature consider themselves quite competent to decide all such problems very promptly. The tendency of nature is not always to restore the former balance, but sometimes to establish a new one." (Henderson and Craig, 1932)

Southern (1948) concurs: ". . . A favorite thesis was that destruction of predators interfered with a mystic 'balance of nature,' and, though it was not clearly stated how this balance was achieved and maintained, it was nevertheless strongly asserted that tampering with it must bring disastrous results.

"A little thought will show that whatever balance may exist in populations of British animals, it is not a 'natural' one in the sense that it represents a prehistoric condition, since cultivation and settlement have already turned any such condition upside-down. Furthermore, as Elton was one of the first to emphasize, some animal communities live in a condition of continual and violent oscillation of numbers. Such fluctuations may be rhythmic (e.g. snowshoe hare, lemming, etc.) or they may be aperiodic (e.g. house-mice, defoliating caterpillars, etc.), but they are undoubtedly natural, since they are a marked feature of the least disturbed of the world's vegetation zones, namely Arctic tundra."

Elton (1930) is even more emphatic: "The 'balance of nature' does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude. Each variation in the numbers of one species causes direct and indirect repercussions on the numbers of the others, and since many of the latter are themselves independently varying in number, the resultant confusion is remarkable."

And Goldman (1925) views the lack of balance in terms of human economy: "However, man has already so profoundly disturbed the equilibrium throughout the civilized world that he must ultimately assume effective and intelligent control of all wild life, utilizing natural enemies of injurious species so far as possible, but keeping them under his direction and supplementing them by all the various artificial agencies at his command."

(2) *The "sanitation effect" and the maintenance of sporting qualities in wild game.* Predators are believed to perform a valuable service to prey species by eliminating the diseased,

crippled, and unfit thereby contributing to the health, physical stamina, and perhaps the survival of the species. Also, because the unwary, slow, and stupid individuals are killed most easily by predators, and are thus eliminated as fast as they are born, the sporting qualities so desirable in a game animal are believed to have developed as a result of this selection.

Nagel (1947) defends this point in favor of predators by saying: "Predation is nature's way of doing for the wild creatures what culling, sanitation, and selective breeding do for tame flocks and herds. This is true of game as of other species. It is the way by which game maintains the sporting qualities of strength and wildness that make hunting and fishing so worthwhile." And this same view is reiterated by Taverner (1939): "The natural predator by unconscious selection captures, on the average, the weaklings and least efficient. Thus both help to build up the constitutional stamina and resistance of the residue by the elimination of the unfit. The sportsman on the contrary endeavors to take the best of the hunted—the largest goose, the highest plumaged bird, the deer with the greatest antlers or the biggest and finest bear, leaving the culls to perpetuate the species.

"The conclusion seems plain that the predator occupies an essential position in the scheme of nature that cannot be replaced by any other agency: that probably one of the greatest disservices man can do for the game he hunts is to destroy his rivals, the predators, the agents that exercise the only selection that compensates for his own deteriorating influence."

And according to Grange (1949): "It has been proved beyond doubt that injured, weak, diseased, incapacitated and subnormal individuals succumb to predation ahead of the strong and healthy individuals. *Not all prey taken by predators is subnormal.* Any such conclusion would be erroneous and at variance with field experience. But among the individuals which are captured and killed by predators are many if not most of the incapacitated animals if a reasonable population of predators is present. To a certain extent, therefore, predation is selective. In eliminating diseased prey individuals, predators not only feed themselves but afford some protection to the prey species itself."

But even on this point, which at first glance appears to be an indisputably beneficial effect of predation, there is not complete accord. Gabrielson (1941) comments: "One statement frequently made is that predators render a useful service to game species in destroying sick and weak animals, thereby helping to maintain the vigor of the stock. There is not much definite evidence to substantiate such assertions, although they are widely advanced as a reason for the protection of predators."

In the same line of thought, Goldman (1930) says: "Another idea that appeals to some, and may even be accepted as demonstrated truth, is that predatory animals are an essential part of nature's plan to eliminate the unfit and maintain wild life at a high physical level. My observations in the field have led me to the conclusion that this alleged beneficial effect of predatory animals may be greatly exaggerated, although having to cope with predatory animals may have had some bearing on the evolution of a race. In modern human society medical science and care lavished on the unfit may cause deterioration of the race, but the conditions that must be met by wild life tend to eliminate the unfit in any case. Many insular species, beyond the reach of predatory animals, appear to be as physically fit as their mainland relatives.

Even the assumption that predatory animals more often attack the unfit should be examined with care for we find in the field much evidence that the strong and healthy as well as the weaker animals are killed. Some have advanced the theory that sick animals and birds are singled out and killed by the predators, but such individuals are apt to be motionless and therefore overlooked as it is motion that quickly reveals location."

And Marston (1942) in his study of bobcat-deer relationships reveals that ". . . The toll is not limited to young or weak individuals; some cats perhaps kill wantonly more deer than they can utilize. . . . Smaller bobcats are fully as harmful to deer as larger ones. Bobcats are not selective in hunting; ordinarily they kill any deer they are able to approach."

The writer can list at least three additional refutations to the value of the sanitation and culling service: (1) Especially during severe winters when a food shortage caused by deep snows or ice storms may weaken game animals so that they become more vulnerable, predators may kill many individuals which would have otherwise survived the period of "fast" and recovered fully. (2) Part of the sanitation effect is nullified by the spread of rabies, mange, tularemia, and perhaps other diseases to prey populations. (3) There is considerable doubt that the admirable quality of "wildness" in game animals comes solely or entirely from the constant harassment by generation after generation of predators. Ruffed grouse in central Canada show little or no fear of man and lack the sporting qualities of grouse in the United States in spite of the fact that they have been subjected to predation throughout their existence. Early colonists reported similar behavior for the wild turkey. Evidently man is the most powerful force in developing a "sporting" game animal. It was *his* constant harassment which has made the grouse, the wild turkey, and the deer truly "wild" in the sporting sense.

(3) *As an aid in the control of rodents.* No one can deny that predators kill and eat many, many millions of harmful rodents each year, and, in so doing, perform a vital service to humanity. The total value of this accomplishment, if reckoned in dollars and cents, would certainly amount to several, or many, millions of dollars. Therefore, no one disagrees that *certain* predators perform a valuable service in reducing the populations of *certain* rodents. But, like all other generalities concerning predators, there are many who disagree that predators successfully control rodent populations even though those who champion predators vehemently state that they do. There are others who feel that the good accomplished by certain predators in reducing rodent populations is more than nullified by other, non-beneficial activities and that certain rodent species are beneficial in themselves and should not be subjected to serious reduction by predators.

Chitty (1938) points out the outstanding efficiency of the short-eared owl in catching mice but shows that, in spite of this constant drain, mouse populations are little affected: "It is concluded that in one year a Short-eared Owl would certainly eat more than 47 lb. of voles or mice, and probably more than 95 lb. but less than 142 lb. This represents a consumption of food animals that may roughly be stated at 2,000 $\pm$ 50 per cent.

"For a certain area on the Scottish border census figures are available of the Shorteared Owl and vole populations in April, 1933. It is shown that the daily requirements would be met by 0.02 to 0.05 per cent of the vole population. . . . it seems unlikely that at the densities under

Photo Penna. Game Comm.

Large predators, such as the coyote, have been found ineffective in the control of rodents.

consideration the total predation would act as an appreciable check upon the vole population."

Elton (1927) cites other figures: "In 1907, a plague of Microtus completely destroyed 15,000 out of 20,000 acres of alfalfa in Nevada. It was estimated that there were 3,000 birds of prey and carnivorous mammals at work in the plague district, that these would be destroying about a million mice or more every month, and that this made no appreciable difference to the numbers." Pearson (1947) provides further figures: "If each pair of owls covers about one square mile (Griscom, 1942) or 640 acres, then at the average rate of 3.2 mice or shrews caught each night these owls would be reducing the prey population at a rate of more than 1.8 animals per acre per year. This amounts roughly to about 10-20 per cent of the average prey population at any one time."

Evidence of the inefficiency of predators in *controlling* rodent populations is also presented by Shelford (1942): "There are numerous instances where predators, such as the coyote, have remained unmolested and yet the ground squirrel, prairie dog, and jack rabbit problem on these areas have been alarmingly acute. There are areas where rodent populations have been reduced by artificial means almost to the vanishing point and yet, despite the fact that native predators were left alone, the recovery of the rodent population was rapid."

Couch (1928) adds: "While there is no doubt that predatory mammals are a factor in controlling rodents, yet they play but a small part in maintaining the natural balance. Larger factors are involved, and these include seasonal conditions, fecundity of the species, the acts of man in providing abundant food, and the presence of natural and other shelter. On the other hand, rodents the size of ground squirrels, or smaller, are more effectively decreased in numbers by raptorial birds than by predatory mammals. The quantity of rodent remains found in the stomachs and disgorges of individual owls is almost unbelievable.

"Townsend ground squirrels *(Citellus townsendii)* were observed to be exceedingly numerous in the spring of 1927 near La Crosse, Washington. One tract of ten acres was treated with poisoned grain, and two and one-half hours later, 1,132 squirrels were picked up, and three days later 574 dead squirrels were counted on the same field. The presence of coyotes, weasels, and badgers was particularly noted in this section. Two coyotes left the field on the first visit, at least 20 weasels were seen, and badger diggings were plentiful. Hawks were scarce over the entire section.

"The foregoing, though based on limited observations, may indicate that the value of predatory mammals in controlling injurious rodents has been over-estimated, but that birds of prey may be more important factors in bringing rodent pests under control."

Horn (1941) emphatically states: "On all the areas we have studied intensively in California, we have not obtained one bit of factual data which indicates that rodents or rabbits have increased following removal of the coyote." And Poole (1933) agrees: "At no time does it appear that the coyote has applied itself to intensive pursuit of these animals [rodents] or served in any manner as an appreciable control agent."

Whether predators do or do not control rodents, there is another side to the question which is seldom considered. Not all rodents are harmful, and the killing of beneficial species or individuals by predators can be counted against them. For instance, Hardy (1946) describes the benefits of the pocket gopher: "Of the ap-

proximately 246 races of animals reported to occur in Utah, 177 or 72 per cent are rodents, of which a great number are beneficial. One of these which is a pest in the garden, but of untold value in our rangelands, is the pocket gopher. Grinnell of California calculated that annually the pocket gophers in Yosemite move 3.6 tons of earth per square mile to the surface. Burrowing rodents such as pocket gophers form soils because the subsoil is broken and brought to the surface where it is exposed to faster weathering and helps to build our fertile topsoil; weathering of the substratum is hastened by the water and air which enters rodent burrows; snow melts more slowly on porous ground than on hard-packed earth, allowing the water to percolate underground where it adds to sustained flow of trout streams instead of contributing to spring floods; the porous moist soil produces a thicker plant cover which favors water conservation and supports game and livestock; rootlets are better able to penetrate the earth and bring minerals to the plant body which are later stored in the valuable topsoil when the rodents cover the vegetational debris on the surface with earth.

"In the dust bowl of Oklahoma, recent studies show that the greater imperviousness of soils in heavily over-grazed areas is both cause and result of the absence of pocket gophers. Other investigators report that in the deserts of Arizona, pack rats and kangaroo rats change both the physical and chemical nature of the soils in which they live. Each kangaroo rat annually adds to the soil plant nutrients, especially nitrates, that would cost about 30 cents to apply in the form of commercial fertilizer. The function of rodents is thus to fertilize and plow the precious topsoil which supports plant and animal life."

Photo by Maslowski & Goodpaster

Predators destroy millions of mice annually but do not always effectively control their numbers.

At least two of the larger rodents (muskrat and beaver) are among the most valuable of furbearers, and in the East the wood chuck is considered an important game animal. Additional investigation might reveal beneficial activities yet unknown of other rodents presently classified as injurious.

There are many biologists who believe that other factors are far more effective in controlling rodent populations than predation. Among these factors could be listed climatic forces, diseases, parasites, emigration, food supply, and man's own efforts at con-

trol. Goldman (1925) postulates: "It has been asserted by some that predatory mammals exert a beneficial influence in preying upon rodents, thus preventing their abnormal increase and maintaining the natural balance. It is true, of course, that the smaller carnivores, including the valuable furbearers we wish in general to protect, feed extensively upon rodents and thus tend to reduce their potential rate of increase; but there is much evidence that two other important factors limit the number of many rodents. These are, and always have been, the available food supply and epizootic diseases. It is a well-established fact that many rodents tend to increase in numbers locally until visited by periodic outbreaks of disease, which may leave only a few individuals where thousands had previously existed.

"If the food supply is abundant many rodents multiply amazingly in spite of the inroads of predatory mammals. . . . The excessive abundance of rodents in many places under varying environmental conditions forces the conclusion that predatory mammals alone are ineffective in controlling their numbers."

Clements and Shelford (1939) present still another theory: "Let us assume that mice die of old age when about three years old. A favorable year may lead to a saturation of available space. Survival of young will then be limited to the space left by accidental deaths of 'favorable-year' individuals and migration out of the area. In the third year, at a time when reproductive capacity is reduced by senility, more than half of the mouse population dies of old age, causing a sharp decline. Recovery could start only the following year. This hypothesis cannot be tested until some method of ascertaining the age of mammals is determined."

The final consideration in a discussion of predator-rodent relationships is that predators may kill animals which might be better "mousers" than the predator itself. Eadie (1944) in a study of the sort-tailed shrew *(Blarina)* discovered that 56 per cent of 200 shrew scats analyzed contained mouse remains (almost entirely *Micratus).* He states, "The fall population of *Blarina* on this type of habitat was conservatively estimated at three per acre on the basis of trap-removal quadrat studies. Short-tailed shrews might thus have accounted for at least 14-27 mice per acre during the winter months. Circumstantial evidence points to a higher figure. If this represents actual predation, it is of considerable significance in the local microtine cycle."

Perhaps the tiny shrew, working 24 hours each day, kills more mice than many of the hawks and owls, but, because its good deeds cannot be observed and its services lack the glamor of the swooping hawk, it has few defenders among the "protectionist" group. Even though it may be one of the most beneficial of all animals because of its diet of insects and mice, food habits analysts commonly list it with mice and other harmful rodents in evaluating the good and bad qualities of a predator.

(4) *As an aid in the control of insects.* Predators undoubtedly do consume vast quantities of insects and in so doing may aid in some small measure in the control of these invertebrates, but it is illogical to think that predatory animals are an important factor in the control of insect populations. It is true that skunks may dig insect larvae from the ground and help save grass, clover, alfalfa, or other forage crops, and that other predaceous animals may accomplish much good on limited areas. At any rate, it is safe to say that this feeding tendency is a desirable one and should add to the economic value of insectivorous predators.

Several economic biologists warn

that this service should not be overemphasized. McAtee (1913) states: "When we consider the degree of insect control necessary to the commercial success of crops, it is evident that man must almost invariably depend upon his own efforts. We must know about natural enemies, give them all due credit and protect them, but we must beware of exaggerating their services. People are too easily misled in this direction, but the final result of too great faith in natural enemies is disappointment."

And Gabrielson (1941): "For example, enthusiastic bird conservationists are prone to exaggerate the value of the insect-eating habits of birds [includes all birds, not just predaceous birds] and their practical benefit to the human race. There is no question that the insectivorous birds on this continent consume enormous quantities of insects, and impressive figures showing the number or volume thus consumed, based on accurate measurements of stomach contents, can be quoted to show how many insects are destroyed in a given period by an individual bird or by the total population of birds on a certain area. Statements of this nature, coupled with the assertion that insects would entirely destroy the sources of human food if it were not for the birds, tend to present erroneous impressions that are not based entirely on fact. Entomologists generally consider that adverse climatic conditions, parasitic insects, and diseases are factors of more value in controlling insect populations than are birds, and they produce considerable evidence to support their position.

"Regardless of which may prove to be the correct view of this complex and intricate relationship, it is certain that the insectivorous proclivities of birds are one factor in controlling insects—probably most effective in slowing up an increase in numbers when insects have been reduced numerically by other means—and that because of the pressure thus exerted, the birds should be left to pursue that avocation unless they otherwise adversely affect man's interests."

As in rodent control, predators by killing shrews, moles, small birds, and other prey, may be removing animals which individually are more capable of consuming larger quantities of noxious insects than the predator itself. It is almost certain that the several to many shrews which may be killed by a red-tailed hawk each year will take many times more destructive insects than the few grasshoppers and caterpillars consumed by the hawk in late summer and early fall. In the long run, predators as a group may actually be a factor in the prosperity of insect populations.

(5) *Fur value.* It is estimated that the fur trade at its peak in the United States had a value of approximately $100,000,000 annually. However, at present prices, the value probably averages nearer $50,000,000. Of this figure, one-half or more would probably arise from the sale of the furs of carnivorous mammals. In other words, even at present prices, predatory mammals provide an annual income of at least $25,000,000 for trappers and hunters of the United States and many millions more for tanners, furriers, and retail merchants. This is a big industry, and is unique in the sense that the income is distributed among so many thousands of people of all ages.

Few who object to the control of predators can find fault with a legitimate and managed annual take of furs. They can, and do, object to the taking of fur animals in large numbers at times when the fur is unprime. Of course, it is often necessary to remove an individual furbearer which may be killing livestock or destroying game, but large-scale destruction of these valuable animals

during off-season vermin control campaigns by sportsmen's groups or by concerted trapping or hunting for bounty appears to be an inexcusable waste of a natural resource. However, this apparent truth is often tempered by economic conditions. At the present when long-haired furbearers such as foxes, coyotes, bobcats, raccoons, skunks, opossums, and others, are almost worthless on the fur market, it may be a worthwhile sacrifice to eliminate the excess of these populations at any season to alleviate losses to game and livestock. When the incentive of high fur prices is lacking, other means may be necessary to keep some carnivorous animals within reasonable bounds.

At least there is almost universal agreement that the bulk of all furbearers, under ordinary conditions, should be harvested when the fur is prime by trappers and hunters who are remunerated only by the value of the fur and the recreational pleasures they receive. If properly managed, and if fur prices remained good, the fur harvest should continue at a high level. The populations of preda-

PGC Photo

The recreational value of predators cannot be overemphasized. Crow shooting is enjoyed by thousands.

tory mammals should be sufficiently reduced before the breeding season so that game and other valuable wildlife can reproduce in comparative safety.

(6) *Esthetic and recreational values.* In the final analysis there may be little difference between pleasures designated as "esthetic" and those derived from recreational enjoyment when the stimulation in either case comes from the sights and sounds of nature. Esthetic pleasure suggests a more passive participation while recreation infers a certain degree of activity as hunting, fishing, trapping, photographing, etc.

The esthetic appeal of wildlife (predatory or otherwise) may be most manifest to those who know the meaning of the word, but even those who can neither spell nor define it perceive the beauties of nature and are thrilled by them. Whether animals excite the "ohs" and "ahs" of a society matron or the slow grins of backwoodsmen, the pleasures are heartfelt and truly esthetic in character.

Any time spent in the outdoors whether it be an automobile trip, a picnic, a few hours of fishing, or even a walk in the woods, is enhanced by the sight of wild animals. Deer hunters in the East are often more intrigued by the appearance of a wildcat or fox on the "drive" than by the sight of a buck. Deer are common and lack the esthetic appeal that the wildcat possesses because of its comparative rarity. The lucky Nimrod who gets to see a bobcat is the envy of the camp.

Deck (1938) aptly describes the esthetic appeal of predatory animals: ". . . It seemed odd that sporting tradition should decree death for every creature that might sometime eat a game-bird or fish. For modern men don't hunt for meat—they go to the market. They go afield for the fun of the thing. They like plenty of shots, of course, (though most of these may as well be missed) but mainly they want to see wild things. And strangely, while workaday game may flush and fall and be forgotten, a man remembers for long his glimpses of nature's drama played by the birds and beasts we've been taught to hate as vermin."

The recreational opportunities offered by predatory animals is nearly limitless. Hunting heads the list of these activities. Some predators are hunted partially for profit and others almost exclusively for sport. Many thousands, from the wealthy red-coated hunter riding to the hounds to the mountaineer who "runs him for his hide," are champions of the fox chase. Other thousands insist that there is nothing to equal the nocturnal sport of 'coon hunting. The coyote is coursed with fleet-footed greyhounds and wolfhounds and is a favorite target of the "varmint" hunter equipped with a high-powered rifle and 'scope. The bobcat and mountain lion are "treed" with hounds. The skunk and possum, especially in the South, are a source of much pleasure for night hunting. The crow also has its following, and millions of rounds of shotgun ammunition are expended by those who delight in this superb wing shooting. A few woodsmen have learned to call horned owls, foxes, coyotes, and hawks and pursue this sport with all the enthusiasm of a hunter calling wild turkeys.

Trapping is another form of recreation made possible by predatory animals. Some trap almost exclusively for the monetary return, others trap partially for profit and partially for recreation, and a great many are motivated principally by the recreational benefits. Fur animals provide a type of recreation which is healthful, enjoyable, educational, and profitable.

Still others derive considerable gratification from photographing wild predators. Many are content to

while away the hours observing their habits and homelife.

So whether one is vigorously pursuing a fox at full gallop or merely lying peacefully on one's back in the warm summer sun watching the lazy circling of a hawk against the sky, the enjoyment is real and the satisfaction tangible. *This is an undisputed blessing provided by predatory animals.*

(7) *Scientific values.* Dice (1925) makes it clear that predatory animals are equally as important from a scientific standpoint as non-predatory forms. He says: "Any species of animal which is the sole living representative of its group is of great scientific importance as being a unique type. On the other hand, all the species and subspecies which together constitute a series of closely related forms are also of high scientific value, for, by the critical study of such groups of closely related forms, we can secure important evidence about the process of organic evolution and about the factors concerned in causing evolution."

Later he adds: "The lives of all species of animals living in one locality are closely interrelated; especially close are the relations between the carnivores and the forms on which they prey. All of these associated forms, predatory and non-predatory alike, have evolved under mutual adjustment, and all of these associates must be considered together in any attempt to explain evolution or distribution. With the predatory mammals eliminated it will become more difficult to explain the origin of many adaptive structures and habits in the remaining species.

"The explanation of the facts of evolution and of distribution are among the most fundamental problems of biology, and for their solution we shall need the greatest completeness of knowledge about all possible kinds of animals. The world, therefore, cannot afford to permit the elimination of any form of wild life without the most urgent economic reasons, as determined by the most careful investigation.

"I do not advocate that predatory mammals be encouraged nor permitted to breed everywhere without restriction; but I am sure that the extermination of any species, predatory or not, in any faunal district, is a serious loss to science."

(8) *Forest reproduction and watershed protection.* Grazing and browsing animals, especially deer, but also other members of the deer family, rabbits, and rodents, are capable of seriously suppressing forest reproduction and of endangering the water-holding capacities of watersheds when the range becomes overpopulated. These have been two of the most insidious economic repercussions where big game herds have been permitted to increase beyond the optimum carrying capacity of the natural forage supply. In Pennsylvania, the tremendous deer herd at its peak was probably destroying more timber of potential commercial value in a year than forest fires. In California and other mountainous states, serious permanent damage to watersheds has been caused by superabundant grazing and browsing animals.

Palmer (1898) presents a poignant lesson in the dire destruction which can result from overbrowsing: "The historic island of St. Helena was, at the time of its discovery, covered by a dense forest. More recently it has been described as a comparatively barren, rocky desert, because of its devastation by goats (introduced by the Portuguese) which, within 75 years, increased to thousands. They browsed off the protective cover of vegetation, exposing the soil of the steep slopes to erosion, and soon bare rock replaced the wooded hills."

It is not inconceivable that a similar fate awaits large areas of the United States if herbivorous animals

are not held in check in some manner. Where a population of this kind is not harvested adequately as a game crop for hunter's recreation, natural predation should be encouraged to aid in control of such populations. This can be one of the most valuable contributions of predatory animals to man's economy.

(9) *Control does not necessarily increase game populations.* The title of this portion of the report is probably misleading, because, so far as the writer knows, no one has ever defined "control" in terms of predation. Does control means complete extirpation of all predatory animals, or only certain species, or of only individuals of certain species? Or does control mean a satisfactory reduction of number of all species, of certain species, or of individuals of all or certain species? And is "satisfactory reduction" accomplished by removing 10 per cent, 30 per cent, 50 per cent, or 90 per cent of the entire predator population, or should 60 per cent of one species and 20 per cent of another be removed?

From this it can be seen that when some investigator reports that "predator control did not cause an increase in game populations," it means next to nothing. In the first place, has anyone ever demonstrated the ability to *control* effectively all predatory species over an extensive area? They reduce the predator population, quite effectively for some species, but others, often the most destructive, escape almost untouched. Edminster (1939) attempted to control predators on a tract in New York, but after removing one carnivore for each four acres of the study area reported: "Records of predators taken the second year indicate that elimination was markedly successful on the long-eared owl, red-tailed hawk, and small brown weasel; moderately successful on the horned owl, marsh hawk, and crow. Species that showed little or no reduction the second year included the Cooper's hawk, sharp-shinned hawk, sparrow hawk, red fox, gray fox, skunk, domestic cat, red squirrel, and raccoon."

Other investigators, even with much expert assistance, have encountered similar difficulties in attempting to control predator populations on large tracts. There is a constant influx from surrounding areas, and those which escape capture are often the older, wiser individuals which are probably the most capable game destroyers. *Complete control apparently can only be accomplished on small areas where specially-constructed pens exclude all predators, whether avian or terrestrial.*

The important thing to consider where studies have indicated that predator control has not increased game populations is: *has there actually been control? A substantial reduction of predators does not necessarily mean reduced predator pressure!* In the work of Edminster cited above, the almost complete elimination of long-eared owls, red-tailed hawks, and small brown weasels may have had little or no direct effect upon nesting success or chick survival of ruffed grouse, but indirectly, because all three are known to kill large numbers of small rodents, they may have actually contributed to nesting success had they been permitted to live (red squirrels commonly steal eggs from grouse nests—King, 1937). Stoddard (1931) found that a reduction of marsh hawks, which were presumed to be natural enemies of bobwhites, resulted in an increase of cotton rats which were collectively of much greater importance as quail predators (eggs) than the marsh hawks. Thus, the continued presence of marsh hawks, in spite of limited predation, contributed to the prosperity of the bobwhite.

Even among predators which are known to prey directly upon the eggs, young, or adults of any species, sub-

stantial reduction does not necessarily mean reduced predator pressure. It is thought that a certain percentage of a prey population is vulnerable to predation because it occupies precarious portion of the habitat, and it is believed that this percentage can just as effectively be eliminated by a reasonable number of potent predators as it can by twice that number. In other words, *moderate reduction of predators may have little or no effect upon the ultimate prosperity of a prey species.* Errington (1936) found: "Contrary to what would seem most reasonable at first glance, lower population of the most formidable predatory types, down to scarcity or actual absence on the observational areas, has *not* resulted in any appreciable lessening of the net pressure of predation upon bobwhite winter populations."

A concrete example showing that predator reduction does not necessarily cause a decrease of predator pressure is given by Lehmann and Fuller (1943). In 1942 on a study area of 960 acres (Texas) with a quail population of one bird per 2.52 acres, only about 5 nests out of every 100 were succeeding. Among 50 nests finally located, coyotes destroyed 26 (52%) and accounted for 274 eggs out of 559 (49%). Fall trapping and accurate age determination of more than 2,600 quail showed a ratio of 2.2 young to each adult. The ratio of young to adults, according to the authors, would have been approximately five to one except for heavy nest losses, presumably by coyote.

Then in 1943 in their own words: "Approximately 762 quail, 1 bird to about 1.2 acres, began nesting on the 960 acre study area on the Jones Ranch in late March, 1943. From May 11 through June 1, 50 active quail nests were found in or near this area. The clutches were large containing from 8 to 24 and averaging 14.8 eggs each. The weather was favorable; nesting cover was luxuriant. State predatory animal trappers had taken 632 coyotes and 35 bobcats from the Jones Ranch and surrounding ranches the previous winter, and the animals were definitely not abundant. In other words, prospects for a bumper quail crop were excellent. These prospects were soon to be dimmed, however, by those coyotes which did remain.

"By June 15, in fact, coyotes had destroyed 28 of 50 study nests, or 56 per cent. They definitely killed 5 adult quail on the nest and probably killed 2 others. Six nests (12%) were terminated by skunks; one is still incubating. Only 15 nests (30%) hatched.

"The impression of nesting success conveyed by the 1943 nesting studies (30% hatch) is overly optimistic. Forty-eight of the 50 study nests were incubating when found. Since egg loss is always heavier when quail are laying than it is when they are setting, it is apparent that the over-all loss of quail eggs was more than 2 nests in every 3. Actually, only about 10 per cent of the adult quail, rather than 30 per cent, now have young."

For studies designed to measure the value of predator control as a management practice for increasing game populations, it is recommended that control be selective and intense and that, if game populations do not respond to this control, hasty conclusions should not be accepted until it is definitely known that predator pressure had been alleviated.

Even though the above discussion would seem to be intended to refute the statement that "predator control does not necessarily increase game populations," there are many instances wherein predators are not the controlling factor in game populations and, therefore, predator reduction can have little or no value. During the decline of ruffed grouse, snowshoe hares, and other cyclic species, predator control appears to offer

little assistance in preventing the crash. Where food, or water, or other "necessities" are lacking, predator reduction cannot prevent a prey population from falling to the level set by a more restrictive controlling factor. And in the words of Hamilton (1937): "We have seen that wholesale destruction of predatory species does not often accomplish the anticipated end result of favoring game increase. The disturbance of Nature's equilibrium sets in operation a host of unlooked-for consequences. Each animal in an ecological complex is closely related to its neighbors, the whole making up an elastic web which, if but slightly disturbed, makes for great, and frequently grave, consequences."

(10) *Predators remove only surplus game over the "carrying capacity" of the habitat.* A theory has been advanced which states that only that proportion of a prey population which occurs in excess of the carrying capacity, or threshold of security, of the range is subject to heavy predation.

What establishes the threshold of security for a particular habitat? Food, cover, and intolerance to crowding have been suggested as prime factors, but to what extent do these limit or alter the capacity of the environment? For example, in the northern states there is ordinarily an abundance of food for bobwhite quail except during the winter and eary spring months. Thus, carrying capacity as governed by food is seasonal in nature, and ordinarily becomes a true limiting factor only during three or four months of each year for this species. If the winter is open, the potential is perhaps two, three, or more times higher than it is when the ground is covered with deep snow for long periods of time. It is known that a single severe winter, or at most two consecutive severe winters, will nearly annihilate bobwhite quail in northern states, and that even over ordinary winters there may be a substantial loss ascribable to climatic factors, or to the sparsity of food and cover caused by them (deep snow).

Food, then, may be an important, although inconstant, factor in the establishment of carrying capacity for bobwhite quail in northern states, but what is the role of food on the southern quail range where losses of adult birds from severe weather, i.e. deep snows and extreme cold, and temporary acute shortage of food are practically unknown? How does the food supply affect prey species living in the North which are relatively immune to climatic forces in the adult stage? The numbers of varying hares, for instance, during the period of cyclic increase are little affected by the food supply until they have reached a near-maximum population. Except during periods of unusual abundance, the food supply appears to have little effect upon the survival of snowshoe hares and other hardy northern animals and probably is not the prime factor in the determination of carry capacity.

What about cover? For most game species, cover is of primary value as protection against predators. For this reason, carrying capacity as established by the amount and distribution of protective cover is almost identical to that resulting from the effects of predation since the severity of reduction by predation is nearly proportional to the quantity and quality of escape cover. Cover can hardly be considered as an important factor governing the carrying capacity of a habitat, because, unless predators are present, it probably has only a minor influence upon the numbers of most game species.

Intolerance to crowding is unquestionably a limiting factor for many animal populations when at a very high level, but it is unlikely that it is important at lower levels. With the present heavy gun pressure, it is

doubtful whether overcrowding is a limiting factor for many game species on most areas in the United States.

If carrying capacity as fixed by the *food supply* varies widely according to climatic conditions, and if *cover* and *intolerance to crowding* are excluded as modifying influences, it would appear that perhaps predation itself is a major factor in the determination of the carrying capacity of land. During winters marked by heavy snows when a shortage of food and the resulting malnutrition may cause a large part of the quail population to become weakened physically and less alert to dangers, is it not probable that many of these subnormal birds, which because of their weakness become more vulnerable to predation, might have survived if predatory pressures had been lighter or non-existent? In this case, which factor exercises the greater degree of control, or, to put it differently, which depresses the quail population to the greater extent? If there were sufficient food to permit the survival of 1,000 bobwhites on an area of land in spite of deep snows, but predators reduce this figure to 600 by removing a portion of the weakened individuals, which is more to blame for the winter loss —the lack of food or predation?

The final conclusion is that the food supply, the vegetative cover, and the intolerance to crowding will all permit the survival of a larger number of game animals when predators are not present than when they are present, and that predation almost invariably magnifies the depressive action of any of the other factors causing a reduction of carrying capacity. To state that predators remove only those animals living in excess of the carrying capacity, which has perhaps already been set by predation in many instances, appears illogical.

(11) *Other game management practices may partially alleviate predation.* No lengthy discussion or detailed account of the "dampening" effect of good cover upon predation is needed. Wildlife biologists are generally agreed that, without adequate cover, prey populations are susceptible to heavy predation, but when sufficient protection is available losses are likely to be comparatively light. Thus, the provision of the proper kinds of vegetative growth is an important means of combating the effects of predation.

Emlen and Glading (1945) say: "Habitat improvement is the offensive arm of a management program capable of making new and permanent increases in the breeding stock; protection is a defensive activity, a fight to reduce the normal pressure constantly exerted on a population by its many enemies. . . ."

It should not be inferred that merely the provision of an additional amount of protective vegetation will invariably result in a decrease of predation or an increase of game. This new cover must be of the proper kind and must be established in the proper places. Heavy cover is of little value if vulnerable prey species must leave it and expose themselves in the open in order to feed. There must be a favorable juxtaposition of food, roosting sites, and nesting sites in relation to the existing protective cover for game species to profit by this management effort.

Habitat improvement may be accomplished in several ways: planting, plowing, cutting, burning, liming, fertilizing, reduction or increase of grazing, and others, but it is beyond the scope of this study to analyze the merits of each in respect to its value in alleviating predation.

When game animals are not properly nourished, their normal vigor and alertness are likely to be diminished and they may become easier for predators to catch. Any management measures which would

insure adequate nutrition for game, especially during the winter months, might measurably reduce the predatory loss. This result may be achieved by permanent plantings, by annual food patches, or by emergency winter feeding.

Other more specific measures may be of benefit. Stoddard (1931) found that the burning of broomsedge fields exposed cotton rats to hawks and owls and thus reduced quail egg destruction by these rodents. Controlled harvests of game during hunting seasons may remove surplus populations which would be lost to predators over the winter.

These are just a few of the ways by which the mortality from predation can be prevented or alleviated by management measures other than direct predator reduction.

(12) *Predators an important factor in the survival of certain prey species.* It seems completely contrary to common knowledge (and certainly to common belief) that predators could be necessary to the survival or well-being of certain prey species, but it appears to be a fact. Even excluding the more obvious relationship, which has already been discussed concerning the role predators play in preventing herbivorous animals from exceeding their food supply, there are other important ways in which predators contribute to the prosperity of prey species.

First, it might be well to review briefly the benefits of predation upon prey populations which have a tendency to increase beyond the limits of their food supply. The reproductive potential of most organisms is tremendous when measured in terms of months or years. Cole (1948) says: "Some of the common fallacies about populations may be resolved by simply remembering that any population must be finite in size. The reproductive potentialities of all organisms are such that, if unimpeded, populations would grow in a manner very like a sum of money placed at compound interest. It has been estimated by Hodge that one pair of houseflies reproducing at their maximum rate could in five months produce enough descendants to cover the earth to a depth of 47 feet. By a slight extension of the computation it may be shown that under the postulated conditions about one year would suffice to make the number of houseflies equal to the number of electrons estimated by astronomers to be present in the visible universe. This is a dramatic but not an extreme case, as many organisms exceed houseflies in reproductive potential."

This potentiality for increase is by no means confined to insects and other smaller animal life. Darrow (1947) states that it is possible for one pair of grouse to produce a population of over 33,000 individuals in only six years, and Grange (1949) extends this expansion of numbers to 2,000,000,000 in eleven years. The possibilities for cottontails, meadow mice, and other fecund species would be even more startling.

From these arithmetical illustrations of the reproductive potential of animals, it can be seen that, if sufficient counteractive forces, of which predation is one, are not constantly at work, the earth would be almost immediately overrun by hordes of animals, the vegetation completely denuded, and perhaps when the devastation had been completed the only surviving life would be microscopic one-celled plants and animals. Predation, then, except perhaps when it conflicts directly with man's interests, should be accepted as a normal and desirable biological function necessary for the continued existence of life on this planet.

In the words of Huxley (quoted from Elton, 1927): "I suppose that most professional biologists think of the relation of carnivores to herbivores, preyer to preyed-upon, al-

most wholly in the light of the familiar metaphor of *enemies;* and of the relation between the two as being in some real way like a battle. The ecologist, however, speedily arrives at the idea of an optimum density of numbers, which is the most advantageous for the animal species to possess. He then goes on to see by what means the actual density of population is regulated towards the optimum; and finds that in the great majority of cases the existence of enemies is a biological necessity to the species, . . . to have the right enemies,' though it can hardly be spoken of as an adaptation, is at least seen to be a biological advantage."

Although the theoretical reproductive potentialities of any animal are never fully realized, except perhaps very temporarily, the fact that "irruptions" and "plagues" do occur indicates that certain animals may at times momentarily escape from the forces controlling it. This brings us to a more practical discussion of the role of the predator in the survival of prey animals. When a prey species escapes from the control of its natural enemies and exceeds the carrying capacity of its range in respect to the food supply, these animals must die in large numbers or emigrate to other regions, often with disastrous results. In either case the reduction may be so severe as to place the species precariously near extermination. Predation may seriously reduce populations, but seldom to the low point reached by animals on "eaten out" ranges. The Kaibab deer herd and the present herds in Pennsylvania, Michigan, New York, Wisconsin, and other states illustrate instances of a game animal escaping from its predators. The starvation losses suffered by these herds is well known.

Another example, not exactly similar but related to the food supply nevertheless, is given by Leopold (1933): ". . . a normally distributed herd of deer on Vancouver Island, after the lions and wolves had been killed off for their benefit, suddenly 'huddled up' on a small part of their original range and overgrazed it. Apparently normal predation had some as yet obscure influence in keeping the deer normally distributed over the range."

Cartwright (1944) outlines another way in which predators contribute to the survival of their prey: "This brings us to the role of the predator. It is obvious that a species with a 3-year life span which produced all its young uniformly in June would become extinct if three successive adverse seasons destroyed the hatch. Hence, predation, by destroying a substantial proportion of the first and second nestings, *staggers the nesting attempts and thus becomes a major factor in the survival of the species.* To be effective, the predation must be substantial, probably not less than 50 per cent of first clutches."

Cyclic species, especially those whose "crash" is brought on by disease or parasitism, may be materially benefited by predation. Elton (1933) describes an instance of this: (from Hamilton, 1939) "In Norway the willow grouse in earlier years used to multiply periodically and every three or four years every sportsman got a fine bag. After these good years the grouse, as they do in America, died off from disease because they had become so populous. At the same time, the Norwegians had a great drive to wipe out birds and animals of prey, eagles, foxes, martens, and other fur animals. As the birds and predatory mammals have become scarcer, it has been noticed that the epidemics among willow grouse have become increasingly worse. Instead of more and better willow-grouse populations having been produced by supposed protection through widespread destruction of predators, the stock of

these birds has become progressively more decreased.

"It was suggested that the reason for this great mortality was this: when a grouse became sick with coccidiosis, it weakened and flew less readily and was thus easier to catch. As a result, in the old days the predators used to catch the sick birds more readily than the healthy birds and so prevented disease from becoming too severe, except after the birds had become very abundant."

Beside these instances wherein predators may actually be necessary to the survival of the species, they may perform a worthwhile service by contributing to the prosperity of others. The oft-quoted example of Fisher (1908) illustrates this relationship: (from Hamilton, 1939) "An extensive marsh in northern New York harbored great numbers of ducks, rails, turtles, and other aquatic life. The snapping turtles deposited their eggs in great numbers in the sands of an old beach bordering the swamp. These delicacies attracted the skunks of the neighborhood, and their feasts so reduced the total output of eggs that only a small percentage of the young hatched and reached the water. As time went on conditions changed. Skunk fur become fashionable and commanded a good price. Within a short time the skunks almost disappeared. When the check on their increase was removed the snapping turtles hatched in great numbers. When their numbers had been naturally controlled by the destruction of a large proportion of their eggs, their food supply was adequate, but when their numbers greatly increased the supply proved insufficient. Finally, through force of circumstance, the turtles added ducklings to their fare until the few ducks that refused to leave the marsh paid the penalty of their persistence by rarely bringing to maturity more than one or two young. At last there came about a depreciation in the value of skunk pelts, with a corresponding loss of interest on the part of the trapper, so that the progeny of the surviving skunks congregated at the old beach and devoured the eggs of the turtles which had enjoyed a brief period of prosperity. This, coupled with the destruction of the turtles by market hunters, attracted more ducks and the old marsh again became a populous center for gamebirds."

And the bluejay, which is notorious for its egg-stealing propensities, was found by Lay and Siegler (1937) to be a real asset to bobwhite quail in Texas: "The number of acorns made available to quail by bluejays is so great, that the jay is very likely the most important link between the acorn and the quail in woodland type as exemplified by Walker County, Texas."

Hamilton (1937) gives still another example: "We yet know little regarding the relations existing between the mouse millions and game birds. What has been recorded indicates that the food of the little deer mouse is similar to that of the grouse. One mouse will store a peck of beechnuts or several quarts of clover seeds. Various small mammals, which frequently number more than one hundred to the acre, are potentially very important competitors of game birds for the available food supply. Fortunately their numbers seldom get out of bounds, for alert foxes, weasels and other predators are always ready to grab them up."

And still another example of indirect benefit of predator to prey: It is said that on some English heaths, an overabundance of rabbits causes the heather to be replaced by grasses or bracken, both of which are of little value as food or cover for Scotch grouse. Thus, a reduced rabbit population as may be maintained by reasonable numbers of predators might contribute to an increased Scotch grouse population.

Arguments Favoring Predator Control

(1) *Livestock and poultry damage.* It is useless to cite a large number of examples of recorded economic loss from predation, because the fact is accepted, and well known, that predators do cause a monetary loss to farmers, ranchers, and poultrymen running into several millions of dollars annually. The literature is full of these figures. For instance, Goldman (1930) states: "In 1915 and 1916 the losses of livestock from rabid coyotes in Nevada alone were estimated at $500,000. Four hundred head of cattle were reported to have been killed on one ranch." And later he adds: ". . . National Forests, where 100,000 head of sheep were killed by predatory animals last year (1929) according to figures compiled by forest officers, . . ." Latham (1943) says; "The annual poultry loss from fox predation in Chester County (Pennsylvania) alone is conservatively estimated to exceed $20,000 and proportionate damage is suffered in each of the other counties of the study area." Whether on the sheep and cattle ranges of the West or on the poultry "ranges" of the East, predation takes a constant toll of the flocks and herds.

Protectionists advocate preventive measures instead of predator control to alleviate this loss and there is much merit to many of their suggestions, but it is not economically practical, nor possible in many cases, to exclude predators with wire fencing, frightening devices, more herdsmen, or other expensive measures.

Gabrielson (1941) capably summarizes the problem of predation on livestock in this way: "The practical side of this matter is that there is a definite loss to the livestock industry, usually felt most severely by the small operator, and that this loss is direct and visible and very frequently a serious matter to the individual concerned. It is inevitable that some sort of human control will be exerted, but a compromise between extremists as to the proper degree and scope is difficult to arrange. Sane handling of the problem obviously lies somewhere between the total extermination desired by the outraged stockman and the no-control idea of the detached nature lover.

"It is always to be kept in mind that the destructive effect of the predation here discussed is not so much upon the total population of domestic animals as upon the economic welfare of human beings dependent upon these populations. For example, coyote activities might never completely destroy or even greatly reduce any certain band of sheep or flock of turkeys, and yet they might seriously affect the livelihood of the families dependent upon them. The margin of profit, which must furnish that livelihood, is usually small and a very modest loss may wipe that out.

"In such circumstances, the problem becomes not one merely of animal interrelationships but of economics and human economic welfare as well. So long as it is necessary for man to tend his flocks in regions seriously infested by predators, some form of control will be exercised. Theorizing as to natural balance of animal populations in the world will not change the fact. The only questions are, how much control is necessary and how shall it be undertaken? On both these questions there is much room for argument. A fair examination of this phase of the wildlife problem makes it obvious that control is necessary in some areas and that in others no control is justified. There is also a borderline zone between the two where differences of opinion will always occur between the advocates of drastic con-

trol and those believing in little or no control."

(2) *Increased game populations for recreational purposes.* Since most of the so-called "protectionists" or "nature lovers" and even some of the professional biologists still insist that "in no instance has it been shown that predator control has caused an increase in game populations," several actual examples of increase, picked at random, will be presented.

Goldman (1925) speaking generally says: "The disastrous effect of predatory mammals on game has been clearly demonstrated, but not always fully realized. In various parts of the West, where through systematic efforts the predatory mammals have been greatly reduced in numbers, there has followed a marked increase in deer, wild turkeys, sage hens, quail, and other game species. . . ."

Speaking more specifically of coyote-deer relationships in California, Horn (1941) states: "After coyote removal, there was an increase in fawn survival each year. In brief, this study shows that coyotes on this area feed largely upon deer, and that the removal of the coyote has resulted in increased survival of fawns with an increase in the younger age classes of deer."

A recent Outdoor News Bulletin (1949) carried the following release: "Antelope fawn survival has been found by the U. S. Fish and Wildlife

PGC Photo

When a game animal no longer has any important natural enemies to remove the surplus, it may increase to such an extent that it "eats out its range" and the surplus is lost through starvation. This is the history of the white-tailed deer in many states.

Service to be directly proportional to the extent and effectiveness of coyote control in several states, . . .

"On Arizona ranges where scientific methods of control has been employed, a fawn survival rate of 94 per cent was recorded; where no control was used, survival was as low as 21 per cent. In Alaska, the Service's stepped-up control program already has been reflected in increases in moose, caribou, deer, mountain sheep, and reindeer. Stockmen also have benefited. Albert M. Day, director of the Fish and Wildlife Service recently stated, 'In many parts of the West, from New Mexico to Montana, where losses formerly ran as high as 15 per cent, sheep are now being ranged without herders and without losses from predators." Control of stock-killing coyotes in many areas is saving farmers and ranchers millions of dollars."

Gabrielson (1941) adds more information on antelope: "An outstanding example of the effect of predator control occurred with the upswing of the antelope herd in the territory adjoining the common boundary point of Nevada, Oregon, and California. In that region a small herd remained in 1920 and 1921, when the species had reached its lowest ebb there. The antelope were protected by state game laws, and there is little evidence that any considerable number were killed illegally. After their low point in 1920, when the animals had decreased noticeably from disease and possibly other causes, predator control operations were undertaken by the Biological Survey, and between January 1, 1921, and June 30, 1934, a total of 7,595 coyotes and bobcats were removed. While the reduction of the predator population was being carried on, the antelope herds, which had for several years been stationary, with comparatively little success in rearing fawns, gradually increased from about 500 animals to their present population of 7,000 to 8,000. Now the antelope are numerous enough for the same or even greater predator pressure to be of less importance than formarly, and other factors affecting the herd may become more serious."

Another example of big game response to predator control is given by Hamilton (1939): "Formerly a policy of exterminating all predators over a 40-year period so favored the deer, bighorn, and mountain goats that these animals had by 1920 become a serious nuisance and even a

In the South, it was found that marsh hawks actually benefited bobwhite quail by catching the cotton rats which destroyed their nests.

PGC Photo by Brown

threat to human life. After hundreds of bighorn had been trapped and shipped to restock depleted areas in the United States and Canada, the menace of overpopulation continued. The sheep actually stood on roadside embankments and, as motorists drew level with them, attempted to leap over the cars. These leaps ofter fell short, with attendant damage to people and cars. Rocky Mountain goats became so numerous that they encroached and took possession of the upper bighorn ranges, driving the sheep to lower valley levels. Deer ran amuck in the city of Banff, destroying gardens and lawns and creating a general disturbance. In an effort to reduce this excess dangerous population of deer and other big game animals, wardens were instructed to cease killing predatory mammals. Little change was noted for three years, then a perceptible decrease was observed in large game. With an increase in their population due to protection, mountain lions once more became numerous and upon occasion actually entered the city of Banff, where they killed deer and sheep. By 1930 the cougars had so routed the game herds that Banffites were alarmed and predatory-animal control again came into force. With the killing of a number of cougars, the herds have reinvaded the city and undoubtedly will again become a problem if predator control is carried to extremes."

The benefit of predator control to game animals is not confined to larger species alone. Stoddard (1931) was one of the first to demonstrate that selective predator control would increase small game populations (bobwhite quail). His conclusions are: "Perusal of the chapter devoted to 'quail mortality' should convince the most skeptical that natural enemies of the bobwhite must be controlled under certain conditions, if any considerable surplus of birds is to be available for sporting purposes year after year."

Similar results were recorded by Glading, Selleck, and Ross (1945) with valley quail in California: "It is our belief that the intensive local predator control such as was practiced in the years up to 1941 was largely responsible for the high population of quail. This is borne out in part by the fact that in 1942, when predator control was comparatively lax due to the loss of manpower and the illness of the remaining employee, the population slumped badly, even though feeding was continued at roughly the same rate. Unpublished studies of the Cholame Experimental Area (Glading and Ross, ms.) reveal that such intensive local predator control can result in considerable increase in quail. . . ."

Stoddard and Komarek (1941) express the undesirability of excessive predation by saying: "In the Southeast the bobwhite is, for all practical purposes, single-brooded and, while these birds continue nesting attempts from late April to August or September if necessary, they cannot perpetuate and furnish a shootable annual surplus where combined pressure from natural enemies is too great during the breeding season—even though food and cover conditions approach the ideal."

Increases in wild turkey numbers as a result of predator control in Georgia are reported by Riter (1941): "E. A. Schilling, Range Examiner, Southern Region, United States Forest Service, recently reported an interesting observation made on an area comprising some 100,000 acres on the Chattahoochee National Forest in northern Georgia. Much cultural work had been done on the area to provide openings in the forest canopy and artificial food patches for game. The remnants of wild turkeys and grouse that were being fostered were not responding

to the improvements and the protection afforded. Something was wrong. Investigations revealed that bobcats and foxes were numerous: wild turkey bones were frequently noted at bobcat dens; and evidence of turkey and grouse kills by foxes was found. Several bobcats and foxes were trapped and their stomach contents analyzed. The analyses disclosed that grouse and turkey constituted an important part of the diet, thus substantiating field observations. In 1937, after careful preliminary study, a general trapping program was initiated on the area. In order that trapping of the furs should not be wasteful, the season was limited to winter months. During 1937, 126 bobcats and 116 gray foxes were taken, and in 1938, 91 bobcats and 83 foxes. A great increase in the turkey population was noted in the fall of 1937. An additional increase was noted in 1938, but the gain was not so great as it had been in 1937. All factors considered—climate, food, cover, protection from shooting—it was evident that the sudden increase in the number of turkeys was in response to protection afforded against predators. Mr. Schilling also reported a similar result on a 125,000-acre area on the Black Warrior National Forest in Alabama."

And Edminster (1939) found that predator control permitted a 25 per cent increase in the numbers of ruffed grouse in New York when the population was below the carrying capacity of the range, but that predator control appeared to have little effect upon the population during peak years. He suggests, however, that if the study area had not been closed to hunting, and the grouse population had been prevented from reaching a peak, the predator control efforts may have continued to be fruitful

It has been shown that, in some instances at least, predator control has caused an increase in game populations. There are other studies which show, just as conclusively, that predator control did not favor game in-

PGC Photo by Latham

Poultry is sometimes wantonly destroyed by individual predators, but this is often the result of neglect on the part of the farmer.

creases. Why should the same management practice be effective in one case and not in another? If it is definitely known that predators are killing individuals of a game species or destroying the eggs and predator control does not initiate expected increases in the population, there are two possible explanations for this apparent discrepancy: (1) that predation is not the factor effecting ultimate control of the population, or (2) that control has not been complete enough to reduce noticeably the degree of predator pressure.

Ordinarily predatory species are larger and are slower breeders than the species which form their prey. Thus, if a prey population is large, it is difficult for the predator to breed rapidly enough, providing it also is subject to certain population checks, to kill more than a surplus quantity of the prey annually. However, even though this surplus lost to predators may not be important to the continued existence of the species, it may be that portion of the population which man wants to harvest as game or, in the case of poultry or other livestock, to sell for profit. Where a large prey animal is harassed by a smaller predator with a greater reproductive potential, the degree of control may extend well beyond the surplus as was seen in the coyote-antelope-deer relationships described above. Gabrielson (1941) says in regard to this: "The coyote is a much more prolific breeder than these two big-game species and when their pressure is concentrated on the slower breeding forms during the fawning season it may have a definite effect on game abundance, even though there is no predation during the rest of the year. When the herbivorous population is high and predators are in normal numbers, predator pressure is obscured, and, to say the least, its measurement is difficult. Under such conditions predation may well become a negligible factor, and the predators, even though preying to a normal extent on deer or antelope, may still be utilizing animals that are surplus to the existence or even the welfare of the herd."

From the above discussion, it would appear that, if big-game populations are decreased below a certain level, predator reduction may effect a comeback to more normal numbers unless a more potent controlling factor is holding the game in check. On small game, the effect of predation is likely to be less noticeable because of the greater fecundity, but even here it is sometimes possible to increase the shootable surplus for recreational purposes by means of selective predator control, although this is not often a practical venture.

That predator control to increase game populations is a permissible and acceptable management measure is attested to by Stoddard (1931): ". . . Control of competing forms of life is, however, as legitimate and necessary upon lands devoted primarily to game production as upon those devoted wholly to agriculture. . . ." And Gabrielson (1941) adds to this: "Where game birds or mammals are subjected to severe hunting, the addition of the hunting pressure to other adverse factors may quickly reduce the normal population of game. In such areas predators may be a factor of importance, and their reduction may be necessary to a greater production of game."

(3) *Protection to near-extinct prey species.* Since all agree that any species permanently removed from the native fauna is an irreparable loss to science and to mankind in general, it is conceded by most that rigid protection of the isolated remnants of an endangered species is highly desirable. The trumpeter swan is one of these species threatened with extinction. Riter (1941) concludes: "The Red Rocks Lake Refuge in Montana, for instance, supports a large part of the only nesting population of the trum-

peter swan left in the United States. The number of these birds is so very small that it is still doubtful whether the species can be restored. Certainly predation may easily be disastrous and there should be no question as to the advisability of control if predation should occur to any degree whatsoever."

The writer also believes that *just as rigid and sincere protection should be provided for endangered predatory species.*

(4) *Destruction of newly released, artificially propagated game.* This subject should be thought-provoking; for, although the hand-reared game which is quickly killed by predators following release may have cost the sportsmen of the country millions of dollars, there are many wildlife biologists who sincerely believe that predators are performing a valuable service in doing this. These biologists are of the opinion that artificially reared game which is stocked to supplement native wild game may, in the long run, cause a decrease in these wild populations and, consequently, in the numbers available to hunters for recreation. By carrying disease, by hybridizing with the wild stock and perhaps thus reducing the vigor, hardiness, or wildness of the race, by attracting predators, and by other possible known and unknown effects, propagated game is sometimes believed to be of primary importance in the failure of game crops.

But regardless of whether this predation is a service or a disservice, it is believed *that predators probably kill at least 50 per cent of all artificially reared small game released in the United States, and the loss is almost certainly even greater than this.* The writer and others who have had occasion to release pen-reared game have had the experience of seeing a hawk (usually a Cooper's) strike and kill a bobwhite quail, Hungarian partridge, or ringrecked pheasant on its initial flight from the crate. Latham and Studholme (1947) estimated that 70 per cent of 1,000 experimental bobwhites released on a study area in southern Pennsylvania had died or had been killed by predators within the first month after release. Of one release of ten birds, a farm cat deposited nine of the ten (bands and all) on the back porch of the farmhouse within a few days.

English (1934) found 3 newly released Hungarian partridges, from a release of 56, with bands on their legs at a red-tailed hawk nest under observation in Michigan, and Wingard (1949) found the remains of 6 recently stocked ringnecked pheasants at the nest of a horned owl in Pennsylvania. There are many other similar records in the literature.

Pough (1948) sums up the effect of predators upon artificially reared game and the possible indirect influence upon wild game as follows: "The high percentage of stocked birds that vanish a short time after their release suggests that such birds must be excessively vulnerable to predators and recent studies seem to bear this out. Tubbs (1946) reporting on a series of releases in Michigan showed that while 9 per cent of the pheasants released 1 month before the hunting season were later bagged by hunters, the number that survived to eventually be shot fell off very rapidly. Only 6.3 per cent of the birds out 2 months were bagged, 5.3 per cent of the 4-month birds, 4 per cent of the 6-month birds, and only 1.1 per cent or barely more than 1 in 100 of those that had had to survive for 11 months in the wild. If the matter stopped there we could be fairly philosophical about it and simply assume that in any release there was going to be a lot of tame and under par birds that were bound to be weeded out by one method or another. Unfortunately, the matter does not stop here, as there is an increasing amount of evidence to in-

dicate that predators as individuals do not always take those animals that are at the moment most abundant and therefore easiest to obtain. On the contrary, it appears that once a predator has learned how to catch and become used to taking a certain type of prey, it will continue to seek it. To turn loose tame, inexperienced game-farm-reared birds that have never had any parental training in avoiding predators, just as the season's crop of young predators are learning to fend for themselves and are acquiring feeding habits that will influence their choice of food for the rest of their lives, is to ask for trouble. Twenty-seven of a spring release of 98 pheasants in Michigan were found within a month at a fox den or at feeding logs (Anon, 1948). By the time the supply of these easily caught game-farm birds is gone many of these predators will have learned how best to catch a game bird and may have become confirmed in their habit of preying upon them. As a result they are likely to make an extra effort to catch some of the local stock of wild birds in order to continue what has become a well-established feeding habit."

(5) *Harassing effect.* Leopold (1933) summarizes this phenomenon which has been observed and recorded by many investigators including Errington (1936), Stoddard (1931), Latham and Studholme (1947), and others. Leopold says: "One adverse effect of predators apparently not heretofore recognized as important, occurs when predators prevent game from feeding, or otherwise interrupt its normal routine, by confining it to 'escape coverts' or other safe but often foodless places. Even though no actual mortality be suffered, such harassment may have serious indirect effects, especially during critical seasons. Thus during the short days of northern winter when food is scarce, and continuous search for food necessary to keep 'body and soul' together, the confinement of a covey of quail by a hawk for hours at a time may effectively start that cumulative deficit of input over output which constitutes starvation.

"As already mentioned, Errington found that after harassment by a Cooper's hawk, a quail covey may entirely change its previous feeding place, and remain confined to dense 'escape coverts,' not only during the hawk's visit, but for a week afterward. If there be no food within such coverts, the covey must either starve and freeze, or venture forth and be progressively picked off.

"*The Game Survey* (pp. 73-74) found that during the hard winter of 1929-30, most of the quail coveys visited in Missouri were being harassed by hawks, including species probably incapable of catching any but weakened birds. The frequency of evidences of killing by hawks appeared to be inverse to the sufficiency of escape cover (usually osage) at the covey headquarters, and to the food therein (natural, or artifically supplied). The tracks showed the daily cruising radius of each harassed covey to be surprisingly short (often under 50 yards), and usually co-extensive with the escape coverts. All of the visible evidence pointed to the conclusion that harassment of foodless coveys led to their subsequent starvation, or decimation by hawks of some kind, whereas harassment of fed coveys did no visible harm. . . .

"Harassment is not confined to game birds and raptors. I have seen coyotes calmly attending does with fawn, evidently watching for one moment of relaxed vigilance on the part of the mother. It is obvious that the doe cannot feed herself or nurse her offspring in a normal manner while thus attended. . . ."

(6) *Predators as carriers of disease.* One of the most destructive and dangerous diseases spread by predatory animals, especially the *Canidae*, is *rabies.* In an account of an early

outbreak of rabies in the West, Goldman (1930) emphasizes the seriousness of this disease: "In recent years coyotes have been a very serious menace to the human population, as well as to livestock through the alarming spread of rabies, transmitted through them, over several western states. The malady began in central California in 1909, and by 1915 had extended over northern California and much of Oregon, Washington, Idaho, and Nevada. The recorded number of people bitten by November 30, 1923, is over 2,000, of which number 56 died. The prompt application of the Pasteur treatment doubtless saved hundreds of lives. In 1915 and 1916 the losses of livestock from rabid coyotes in Nevada alone were estimated at $500,000. Four hundred head of cattle were reported to have been killed on one ranch. In January, 1922, a new outbreak in Washington was stopped by the concentrated cooperative efforts of Federal, State, and County officials, when 1,800 coyotes had been killed in four counties. In 1923 the disease was suppressed in parts of California, Oregon, Nevada, Utah, Idaho, and Washington, and in the same year it appeared in coyotes and bobcats in Colorado, where, within a short time, four persons were bitten, and livestock valued at $4,000 was destroyed. This has been followed by outbreaks in eastern Washington, eastern Oregon, central Oregon, northern Utah, and sporadic cases at widely separated points in Nevada. Experience has indicated that new outbreaks of rabies may be expected from time to time, wherever coyotes become very numerous." These outbreaks still occur periodically in the West.

Within the past ten years the foxes in the East have become rabid over large areas and have menaced dogs, livestock, and humans. A number of people have been bitten, it has been necessary to quarantine dogs in many counties, and livestock losses have been suffered over scattered areas.

Tularemia is known to occur in gray foxes and probably affects other predatory animals. This disease when contracted by cottontail rabbits, muskrats, bobwhite quail, ruffed grouse, and other game and valuable fur animals, may cause losses of considerable economic importance, but the role that the predators play in the spread of this disease is imperfectly known.

Another disease which appears to be concurrent with high fox populations in the East is *Sarcoptic Mange*, a skin condition caused by a parasitic mite. Although the greatest mortality is likely to be suffered by the foxes themselves, the possibility of infestation of other furbearers and dogs is ever-present.

PGC Photo by Latham

Rabies and other serious diseases can be spread to livestock and humans by predators. Here is a red fox with sarcoptic mange.

THE ECONOMICS OF PREDATOR CONTROL

"An ideal control method would be one cheap enough to be economically feasible, specific enough to control the destructive species without killing other forms, and simple enough for anyone to use with assurance of success.

"To be economically feasible, the method adopted must cost in time and expense less than the damage that would result if no control were attempted." (Gabrielson, 1941)

Predator Control Methods

"Hands Off" System

This is at least partially a return to the balance of nature concept previously discussed. The proponents of this system of control, if it could be called control when man does not interfere, are willing to allow nature to "take its course" and wait for overpopulations of predators to adjust themselves to lower levels naturally. It is true that *most* high, or irruptive, populations of predatory birds or mammals have a tendency to drop, often precipitously, of their own accord. This automatic reduction usually comes as a result of a failure of the food supply or because of disease or parasitism.

If it is admitted that predator reductions are likely to occur without man's interference, providing the populations are abnormally high, it would appear to be a practical method for control. But what are the dangers which may accompany natural control?

If the reduction is ultimately brought about by a failure of the food supply, what has happened to the desirable prey populations upon which the predators have been feeding? Can wildlife managers, poultrymen, or stockmen afford to permit this natural course of events? State game commissions or conservation departments are charged with providing a maximum of recreation for hunters and fishermen, and this can only be done when supplies of game and fish are adequate. Before a superabundant population of potent predators will collapse from a shortage of food (prey animals), it may mean that some game species will be reduced to a mere fraction of their normal numbers. If Pennsylvania had not trapped or shot 95,000 foxes during the two-year period from 1945 to 1947 and had permitted these animals to breed unchecked until a self-initiated "crash" came, what would have been the effect upon the hunting bag of small game by 1948 or 1949 when the fox population could quite conceivably have exceeded one fox to each twenty to thirty acres? In Pennsylvania during the fiscal year 1946-47, there were 6 foxes killed for each quail shot during the regular hunting season; 20 foxes for each wild turkey; a little more than one fox for each ruffed grouse (1945 figure, closed in 1946); one fox for each 4 ringnecks; and one fox for each 30 rabbits.

If the controlling factor is disease or parasitism instead of a failure of the food supply, new dangers threaten. Both coyotes and foxes are subject to epidemics of rabies, apparently when the population exceeds a certain density. Then humans, stock, dogs, and other domestic and wild animals are bitten and die along with the foxes and coyotes. Control by disease is always a questionable device, because the degree of control cannot be regulated and severe reduction, almost to complete extirpation,

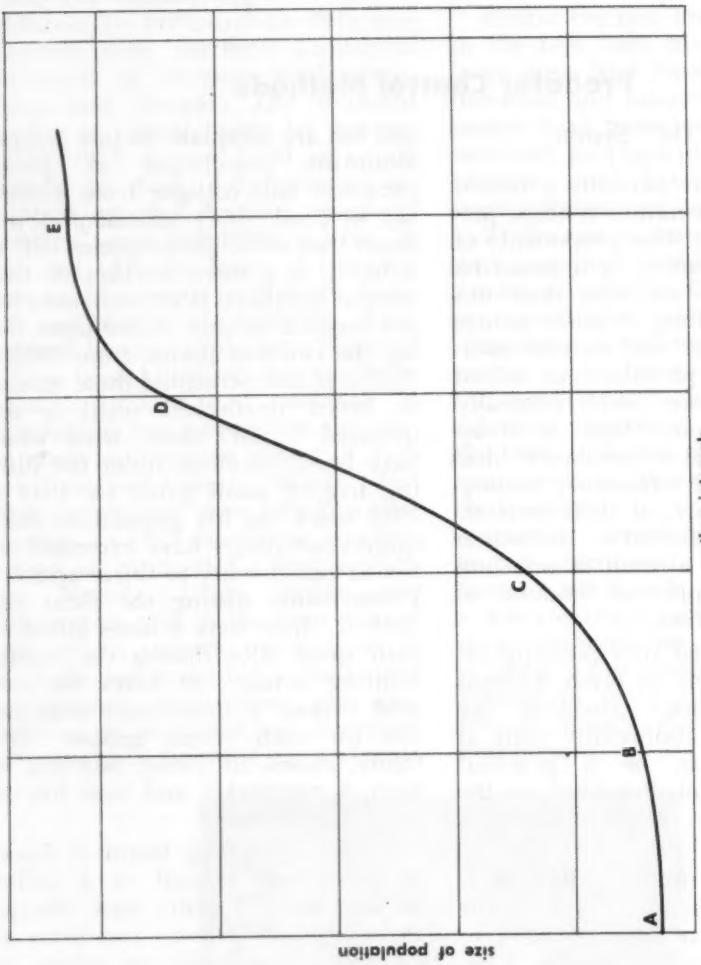


FIGURE 3
Typical Population Growth Curve.

is possible. Of course, the rancher or the hunter may feel that this would be a highly desirable consequence, but many predators are valued for fur, sport, or other uses and so severe a reduction may not be good management.

Avoidance and Prevention

Although strictly not a control measure, *avoidance and prevention*, by accomplishing the same end, may be considered as one. Kalmbach and Linduska (1948) defend this approach: ". . . Through the centuries man has had to combat these unwelcome guests [rats and mice]. This he has done by all conceivable measures of reductional control, yet in modern programs of rat control the philosophy of avoidance and prevention as exemplified by sanitation and rat-proofing have become important and integral parts thereof. If, therefore, it is effective procedure and sound economics to attack the commensal rat (for which no one has demonstrated any pronounced compensatory values) through measures of avoidance or prevention, can anyone challenge the legitimacy of a similar approach to troublesome wildlife species, some of which possess outstanding attributes?"

There are many ways in which the ill-effects of predation upon livestock and poultry have been avoided or prevented—wire fencing to enclose poultry, "vermin-proof" poultry houses, high roosts for turkeys on range, coyote-proof fencing on western cattle and sheep range, the use of lights and frightening devices, and other specialized ways. Predation upon wild prey populations, including game, has been reduced by certain habitat management techniques, by regulated wildlife harvests, and by the control of cats and dogs.

Paid Hunter or Trapper System

Paraphrasing Jacobsen's (1945) objections to the bounty system, it would appear that the principal advantages of the paid hunter or trapper system are:

(1) It permits concentration against individual livestock and game killers.

(2) It permits work when and where most needed, e. g., in the difficult terrain of summer stock ranges, or to protect valuable game species.

(3) It permits control work at all seasons, and not just during the period of the year when pelts are prime.

(4) It provides a means of meeting emergencies, such as rabies outbreaks, or excessive livestock or game killings concentrated in isolated regions.

(5) It insures continued control efforts beyond the point where bounty or fur trappers would find their hunting or trapping efforts unprofitable.

(6) The trapping of the professionals would likely be less indiscriminate than that of the ordinary private trapper, and thus many desirable animals could be saved.

(7) These trappers could teach farmers, ranchers, and other interested individuals the proper methods of trapping predators.

Jacobsen (1945) champions the paid trapper: "Our own association with the predator problem [in Western U. S.] leads us to conclude that a systematic paid hunter plan will bring more lasting results under normal conditions. Paid hunters can be trained in den hunting, in certain tedious and specialized methods, and in the use of quite selective poisoning processes for areas of high predator population and of the recently developed cyanide injector apparatus."

Jacobsen also favors the hiring of hunters and trappers by groups of farmers and livestock companies as practical in the West as a supplement to bounty and government control.

Among the disadvantages, the following may be listed:

(1) Excessive cost, particularly for smaller predators. Few cost figures could be located for the control of large predators, but Hamilton (1946) says: "State hunters have paid their way in controlling the larger predators. California paid a bounty on mountain lions for many years but finally employed a state lion hunter to keep these big cats from becoming too abundant. All accounts indicate that the state-hunter system is more desirable than the bounty."

On the other hand, Marston (1942) states: "There is always the alternative of paid hunters, but personal experience in hunting cats [bobcats] leads the author to question whether a paid hunter could produce sufficient results under all conditions to warrant a full-time salary."

Douglass and Stebler (1946), in reviewing the practicality of the paid trapper system in Michigan, say: "After the repeal of the bounties 1921, a system of state warden-hunters was instituted, which lasted until June, 1934. During this period a total of 14,410 predators (bobcats, coyotes, foxes, and wolves) was reported destroyed, at a total cost of $508,872.13, or an average cost of $35.04. To be sure, large numbers of other animals were killed also by the warden-hunter's traps, guns, and poisons, but these were mostly porcupines, migrant hawks, woodchucks and other species which were beneficial, neutral, or negligible as regards their effect on game. Inasmuch as game was the chief concern of the sportsmen whose license fees paid for the system, they didn't like it. So much dissatisfaction arose that demands for discontinuance of the warden-hunters and renewal of the bounties finally prevailed. . . ."

The cost of fox removal on the Seneca County, New York, fox-pheasant study is given by Benson (1948). See Table 1.

Darrow (from personal letter) explains this table as follows: "This trapping was done as part of an experiment to test the effect of as complete fox control as was possible to achieve. Therefore, trapping operations were continued throughout the winter beyond the time when practical effectiveness could be expected. In connection with fox trapping by State trappers as a means of thwart-

Table 1. Comparison of cost of fox removal at various levels of abundance (1947-48)

Month	*Trapping costs*	*Number days trapping*	*Number of foxes taken*	*Cost per fox*	*Approximate per cent population reduction*
August	$2,354.01	197	133	$17.70	0 to 24
Sept.	2,304.67	190	104	22.16	24 to 43*
Oct.	1,168.22	92	95	12.30	43 to 64**
Nov.	684.04	60	63	10.86	64 to 75
Dec.	774.19	62	27	27.67	75 to 80
Jan.	922.50	71	13	70.96	80 to 82
Feb.	1,014.00	79	14	72.43	82 to 84
Mar.	1,041.70	86	2	520.85	84 to 85
Total	$10,263.33	837	451	$22.76	

* 6 additional foxes taken by private trapper.
** 20 additional foxes taken by private trapper.
Used by permission of New York State Conservation Department.

ing the spread of rabies in this State, the cost per fox taken has been about $16.00. In this operation, trapping has been suspended during the winter when conditions were unfavorable."

In Pennsylvania, seven paid trappers were hired on an experimental basis as of March 1, 1949. By July 1, these men had taken 509 foxes at an average cost of $19.13. At this time the number of trappers was reduced, but by October 31, a total of 1,031 foxes had been trapped at $13.56 per head. Obviously, fall trapping was most productive. Altogether, from March 1 to October 31, 5,676 predators or destructive animals were taken, including red and gray foxes, crows, skunks, opossums, hawks, owls, house cats, stray dogs, weasels, raccoons, porcupines, and snakes at an average cost of $2.46 per animal.

(2) Reduced take of predators. How many paid trappers would be required to take the millions of predators killed for bounty each year? Could enough be hired, at somewhere near reasonable costs, to accomplish the same degree of reduction, providing the same degree of reduction is desirable? For instance, could a reasonable number of paid trappers have taken the 48,000 red and gray foxes that were killed by private hunters and trappers in Pennsylvania during 1946-47 or would it have taken 100, 200, or more? It is doubtful whether 100 trappers could average 480 foxes each, and unlikely that 200 trappers, even if that many could be hired, could take 240 apiece during the year. Even if 200 paid trappers could have killed 48,000, which is doubtful, the total cost of such an effort would probably exceed $750,000. The $4 bounty for the 48,000 foxes cost only $200,000.

(3) Resentment on part of local trappers. Particularly in eastern

PGC Photo

State hunters may be of value in controlling the large predators in isolated areas.

states, individuals who trap or hunt for profit or recreation are likely to resent the competition offered by state trappers. These people feel that the fur should be harvested by the land-owners and local residents of the region, and that the state is literally taking from them the recreation and revenue which is rightfully theirs when paid trappers or hunters are sent into their district. Oftentimes this animosity is expressed by the destruction or theft of traps or other equipment and a general campaign of interference on the part of the local residents.

(4) Even paid trappers and hunters may not all be honest, and, by careful "management" of the predators so that they are not reduced too low in any one area, the unscrupulous trapper can assure the continued "need" for his services.

It appears, then, that the paid trapper or hunter system may be practical and effective for the control of certain large predators, particularly those restricted both in range and numbers, but that this system may be too costly for generalized use in the control of smaller predators which may be quite abundant and widespread. Also, in highly-populated states, the paid trapper may encounter a resentful local population.

"Vermin" Control Campaigns

Of the several possible methods for controlling predators, the cooperative effort of sportsmen's groups or banded farmers, at least as ordinarily conducted, is one of the least desirable, or, as some wildlife biologists view it, one of the most undesirable. Emlen and Glading (1945) express the sentiments of many biologists when they say: "Indiscriminate destruction of predators, as attempted by many enthusiastic and well-meaning groups, is not effective control; these typical short-lived campaigns over an entire township or county do no lasting good, since only a small percentage of the predators living on the tract are ever eliminated and since the normal increase and migration of survivors quickly cancel the small gains made. Furthermore, such efforts usually include any and all hawks and owls, many of which are beneficial rather than injurious to gamebird populations. Although the numbers of useful birds destroyed by such ill-advised campaigns are probably not large enough to do much permanent harm, it is deplorable that sportsmen fail to recognize their natural allies."

As will be shown in a later section of this report, many game protectors or wardens cannot identify the various hawks and owls, even in the hand. The average sportsman or farmer, with very few exceptions, knows only one kind of hawk—the "chicken hawk." In fact, most members of this group are surprised to learn that there are no "chicken hawks" or "hoot owls" listed in bird guides. Further, they believe that the degree of destructiveness is proportional to size—the larger hawks being the most harmful. Of course, on the average, this is the reverse of the true situation.

Coupled with this inability on the part of the participants to distinguish beneficial from harmful predatory species, vermin control campaigns are often conducted without technical advice or supervision. Thus, there is often a spirit of competition, often with prizes for the top scores, and in the enthusiasm of the hunt almost anything that could be considered predacious, or that remotely resembles any predator, may be shot.

Poisoning

Much controversy has centered around the use of poisons in the control of predatory animals. The defenders, in the words of Goldman (1930), say: "While poison is objectionable it is by far the cheapest and most efficient known agent for

dealing with coyotes and various kinds of injurious animals, including the rodents, where they are abundant and conditions are suitable." There is no denying that if large numbers of predators or rodents, for some pressing economic reason, must be removed quickly, the use of poisoned baits, cyanide guns, or other poison techniques is by far the most rapid and most productive method known. Speed, thoroughness, and low cost are certainly arguments in favor of poisoning.

Perhaps foremost among the objections to the use of poison is that valuable furbearers and other desirable birds and mammals often take the "bait" and are killed. This loss is regrettable and should be prevented whenever possible. Trained government and state predator control men are developing techniques by which this loss is greatly minimized, and the objection is not so valid as it was some years ago. A second criticism concerns the waste of valuable fur. If destructive furbearers, such as the coyote, could be controlled to levels compatible with economic interests by trapping or hunting during the season when furs are prime, this would certainly be preferable, but many times the more cunning species cannot be easily checked in this manner. Especially when fur prices are low and the private trapper lacks the incentive to offer much aid in the control of these predators, poisoning by federal or state men may be the only effective means for relief. At least it is illogical to permit a "sheep-killing" coyote to continue its destruction throughout the summer and fall so that its hide might be worth three or four dollars when finally taken during the winter.

Poison should never be used by inexperienced or untrained persons as a control measure. When private poisoners "scatter poisons as if they were hand-sowing wheat," as one writer put it, more harm than good may be done. At one time it was the practice for western cattlemen and sheepmen to carry a bottle of strychnine in their pockets and to "salt" every dead carcass they came across "without any thought of its possible effect upon carnivores in general." (Henderson, 1930)

Continued experimentation may evolve techniques or poisons which are specific for animals needing reduction, and, for certain species or under certain conditions, the use of poison may be an acceptable method of control in the hands of experts.

Hunting and Trapping for Fur and Recreation

Because *fur value* and *esthetic and recreational values* were discussed under the topic "Arguments opposing predator control," little more needs to be said here, except that, *if the numbers of all destructive predatory animals could be controlled to the levels most compatible with the economic interests of man by harvesting the annual surplus for fur or recreation, this would be the most nearly ideal control method of all.*

It matters little to many men whether they hunt for game which they can eat, for fur which they can sell, or for the thrill and trophy which come with hunting the larger predators such as mountain lions and wolves. In any case, it is the recreational enjoyment which they value most, and there are many, many thousands who derive greater pleasure from hunting predators than from the more conventional game hunting. There is no doubt that if proper publicity were given these "off-season" forms of outdoor recreation, other thousands of sportsmen would become converted predator hunters. This would have the double-barreled effect of helping to control predator populations and of satisfying sportsmen in areas where game is not abundant. Oftentimes hunters who have learned to appreciate the

PGC Photo by Latham

Fox hunting is enjoyed by the rich and the poor alike.

sporting possibilities offered by these animals will hunt them in preference to game; thus some of the pressure on game animals may be relieved.

Because fur is an economic asset, a natural resource, and a means of livelihood for many rural dwellers, there can be no question but that the fur-bearing predators should be harvested for their fur at a time when it is most valuable. However, when the market price is poor on certain predators, as it is at present, the financial return may not be sufficient to cause trappers or hunters to attempt large catches. When fur prices are low the private trapper cannot be depended upon for control, and the adoption of some other method may be necessary. This brings up the question of bounties, paid hunters or trappers, vermin control campaigns, poisoning, and other control measures.

Biological Control

About all that can be said concerning the biological control of predators is that practically nothing is known about the subject and practically no studies have been made nor experiments conducted. The introduction of diseases, parasites, or large predators as a means of predator control would be a risky business

even with a tremendous amount of previous research. *This method of control awaits the scientist with a vast amount of knowledge and a vast amount of courage.*

THE BOUNTY SYSTEM—

Advantages

Increases kill of predaceous species. Although some seem to doubt that bounty payments increase the kill of predatory animals, there is definite evidence that at least under certain conditions these payments do materially increase the take. Whether bounties are effective or non-effective in this respect seems to be entirely a matter of economics. If a furbearer is already commanding a high price on the fur market, i. e. red foxes at $10 to $12, the addition of a $2 to $4 bounty may have little influence upon the total number trapped or shot. However, if foxes are selling at $1.50 or $2, the addition of a $4 bounty may make an appreciable difference. In fact, merely raising the price of the bounty is often reflected by an increased effort upon the part of the trapper. The records of Pennsylvania's *notorious* bounty system illustrate this. In 1922, 351 bobcats were killed in Pennsylvania when the bounty was $8, but raising the payment to $15 in 1923 resulted in the taking of 617 cats. Similarly, raising the bounty on gray foxes from $2 in 1922 to $4 in 1923 stepped up the kill from 4,530 to 7,730 foxes. And inversely, lowering of the weasel payment from $1 in 1936 to $0.50 in 1937 reduced the take from over 80,000 to 29,000. When the $4 bounty was removed from the red fox as of July 31, 1949, several professional fox trappers, whom the writer knows personally, simply stopped trapping foxes altogether. Many of these men had caught from 50 to over 100 each season for the several previous years the bounty had been in effect, but they were now unwilling to expend their time, energy, and gasoline to trap almost entirely for pleasure since the fur of red foxes was almost worthless. Some who persisted in trapping gray foxes for bounty were releasing the red foxes they caught in hopes that this fox would be returned to the bounty list in the near future.

Added income for rural populations. Gerstell (1937), speaking of Pennsylvania, says: "The general economic effects of the bounty system are of no small import. The distribution of approximately $1,880,000 in cash over a period of twenty years to thousands of persons living principally in the rural districts has meant much to many farm families and it is upon those very landowners that a large part of the supply of small game must depend for the production of range conditions favorable to its welfare."

The distribution of bounty monies among rural landowners is undoubtedly welcomed by them, but many do not believe that farmers should be subsidized for their part in game production in this manner, particularly when, as in Pennsylvania, the money comes entirely from contributing sportsmen. In any case it is not good management for the conservation department, or the political subdivisions, of states to spend the money of sportsmen or taxpayers merely to provide an additional income for rural hunters and trappers unless the bounty is actually accomplishing the intended purpose —the reduction of livestock losses or the maintenance of shootable surpluses in game populations. The distribution of wealth should certainly be only incidental to the main purposes of bounty payments.

Stimulates interest in trapping and hunting. Perhaps one of the most valuable of the "hidden" benefits is the extra stimulus which moves a boy to buy a half-dozen traps and

begin trapping. Whether he is a farm lad who sets his traps on his father's land, or a boy from town who must walk out into the country, both are being introduced to the many tangible and intangible benefits of the out-of-doors. Any form of motivation, no matter how abstruse, that initiates an appreciation of Nature and causes any member of our modern society to utilize the blessings of outdoor recreation for the preservation of his physical and mental health, can surely be considered a worthwhile contribution.

Educational benefits. Gerstell (1937) lists three possible educational benefits from the use of the bounty system of predator control:

(1) It provides a means for acquainting the many thousands of bounty claimants with the work of the game commission and arouses an interest in this work.

(2) It educates the public to the need for predator control, Gerstell questions the validity of this educational benefit, however.

(3) It teaches the hunters and trappers to distinguish between "good" and "bad" hawks and owls and perhaps reduces the number of beneficial or harmless forms killed.

Investigative benefits—taxonomy, distribution, reproduction, food habits, etc. It is obvious that the receipt of hundreds of thousands of bodies or pelts of predatory animals over a period of many years offers an unique opportunity for research studies. In Pennsylvania, all hawks and owls must be submitted entire within 48 hours after killing and the exact location and date of killing must be given, so that the hundreds of fresh samples are ideal for food habits studies, taxonomic measurements, studies of diseases and parasites, distribution, cyclic tendencies, invasions, and other purposes.

Although only the dried skin of bountied mammals is required in Pennsylvania, the distribution, the cyclic nature, species ratio, species movement, diseases (mange), ectoparasites, and other pertinent information can be secured.

If recognized and properly utilized, the scientific knowledge which can be gained from a study of specimens submitted for bounty may at least partially pay for the cost even though the primary purposes of the bounty are not accomplished. This opportunity for study is of undeniable value.

The Bounty System—Disadvantages

Several of the more important disadvantages of the bounty system will be discussed in some detail. A part of these and others are summarized by Jacobsen (1945):

"Objections to the bounty system:

(1) They do not encourage concentration of efforts against individual livestock and game killers.

(2) They do not encourage work when and where most needed, e. g., in the difficult terrain of summer stock ranges, or to protect valuable game species.

(3) They permit hunters to concentrate their efforts during the season when pelts are prime, and to leave predators unmolested at other seasons.

(4) Their early apparent value in turning in large numbers of animals dwindles until those left for 'seed' build up a population sufficiently large to make bounty hunting profitable again.

(5) They lead to fraudulent practices such as:

(a) Making claims for predators taken outside the paying state or area.

(b) Releasing trapped females to maintain a breeding stock.

(c) Submitting counterfeit or substitute parts of animals not legally eligible for bounty collection.

(6) They encourage theft of animals and equipment from coopera-

tive and other law-abiding trappers.

(7) They do not provide means of meeting emergencies, such as rabies outbreaks, or excessive livestock or game killings concentrated in isolated regions.

(8) The tax imposed to cover bounty payments seems at times to be an extra burden on livestock owners, in that it returns so little in the way of predator control that they feel obliged to hire trappers at their own expense."

Usually ineffective in controlling predator populations (at least as commonly used). Many tables could be presented which would show that bounties do not usually effect a control of predatory populations and numerous references could be given to corroborate this fact, but so many other writers have discussed this point that it seems useless to repeat what has been said so many times before. Those who should like to review concrete examples should read Gerstell (1937), Douglass and Stebler (1946), Hamilton (1946), Callison (1948), Bradt (1943), Jacobsen (1945), and Pearson (1933).

It is admitted freely that, as commonly used, bounty payments do not usually control predator populations; however it is altogether likely that *any predatory animal can be controlled by bounty payments if these payments are high enough.* Again this is merely a matter of economics. If men are able to make more money trapping predators than by more ordinary labors, they will trap and continue to trap so long as it re-

Trapping and hunting for bounty is big business in Pennsylvania. Oftentimes hundreds of pelts are processed daily in the Bounty Office at Harrisburg.

PGC Photo by Batcheler

mains more remunerative than other work. But as predators become scarcer and the total take per trapper becomes less, it would be necessary to increase the bounty to insure their continued effort, but eventually control would be achieved. When the bounty on wildcats in Pennsylvania was raised from $8 to $15 in 1923, the take for that year was 617. Then followed a gradual reduction in the annual kill until by 1936 the wildcat had been nearly exterminated. The bounty was removed completely in 1936 because control had been effected, and normal mortality from deer and bear hunters, from hunting the cats with hounds for sport, and from accidental trapping (mostly fox sets) has kept the bobcat population from showing any appreciable gain since that time. However, this was a moderately-large predator; it had a comparatively-low reproductive potential; it did not possess the trap-shy qualities of foxes, coyotes, and wolves; and there were probably less than 5,000 in the entire state when the bounty was first initiated. During the same time there were probably at least 40,000 to 60,000 red and gray foxes and probably 150,000 to 250,000 weasels.

If the natural environment is sufficiently favorable to permit a predator population to build up to large numbers, the consequent reduction and control of this population is likely to be difficult and moderate bounty payments will usually be ineffective. Unless more individuals of a predatory species are removed by trappers or hunters than are born and successfully reared each year, then bounty payments cannot cause a reduction of numbers. When it is considered that a spring breeding population of 25,000 red fox vixens is capable of producing at least 125,000 offspring, and that, if most of these survive, it will be necessary to remove 100,000 to 125,000 before the next breeding season to prevent an increase, the immensity of the predator control task becomes evident.

Grange (1949) makes an interesting observation concerning the ineffectiveness of the bounty system: "The charge is sometimes made 'We have been paying bounties on Coyotes and Foxes for twenty years, yet we still have Coyotes and Foxes.' This charge, at least, is no reason to condemn bounty systems, for the purpose of control is *never* extermination of a native species. So, if bounty systems have invariably failed to exterminate native predators, this is one good argument that may be offered in their support!"

Indiscriminate — beneficial and harmless species killed by mistake. This is another case where the "innocent bystander" gets killed. Animals not on the bounty list are destroyed in two ways: (1) by being shot by hunters who misidentify the species or who are incapable of identification (confined almost entirely to hawks and owls), and (2) by falling victim to traps or poison set for bountied species.

Not one out of a hundred sportsmen has the ability to identify most hawks and owls in the hand, and fewer still could "pass the test" of identifying these raptors on the wing or sitting at some distance. Even game protectors or game wardens do not qualify. During 1949, the writer tested the ability of a representative group of these men; each had been instructed in identification sometime during his career, all were regularly called upon to fill out affidavit forms for bounty claimants and "pass" upon the hawk or owl presented, and all were expected to participate in the control of predators as part of their official duties. The twenty-eight protectors, representing a typical cross-section, identified an average of 48 per cent of the seven study skins presented. One man *guessed* all wrong, and none of the twenty-eight was able to identify all seven. The

study specimens were all of common, resident hawks, and all were typical of the species. In fact, four of the seven skins were of the three unprotected species in the state.

Baldwin, Kendeigh, and Franks (1932) describe the indiscriminancy of hawk control in Pennsylvania: "As an illustration of the type of results that are obtained when state-wide eradication is attempted of some species and not others, the recent experience of Pennsylvania in 1929 may be cited. A bounty law was passed providing $5.00 on all goshawks taken in the State. Within one year after the law went into effect, 503 birds were taken into the office of the Pennsylvania Game Commission at Harrisburg in order to secure the $5.00 bounty. Out of this 503 birds only 76, or 15%, were goshawks. Over 58% of all the birds taken were of beneficial varieties." (See Table 3.)

They also speak of Ohio's experience with hawk bounties: "Several years ago when a hawk law was in force in Ohio, the township clerk at Wakeman issued 86 bounty certificates. Of these 86 hawks killed, 46, or 53.5%, were sparrow hawks, which is a very beneficial species. This is to be expected in indiscriminate shooting of hawks, since our census indicates that 50.5% of all hawks which one may meet in the field belong to this species. . . . Control measures designed to eliminate certain species and not others are distinctly and unquestionably *inadvisable*."

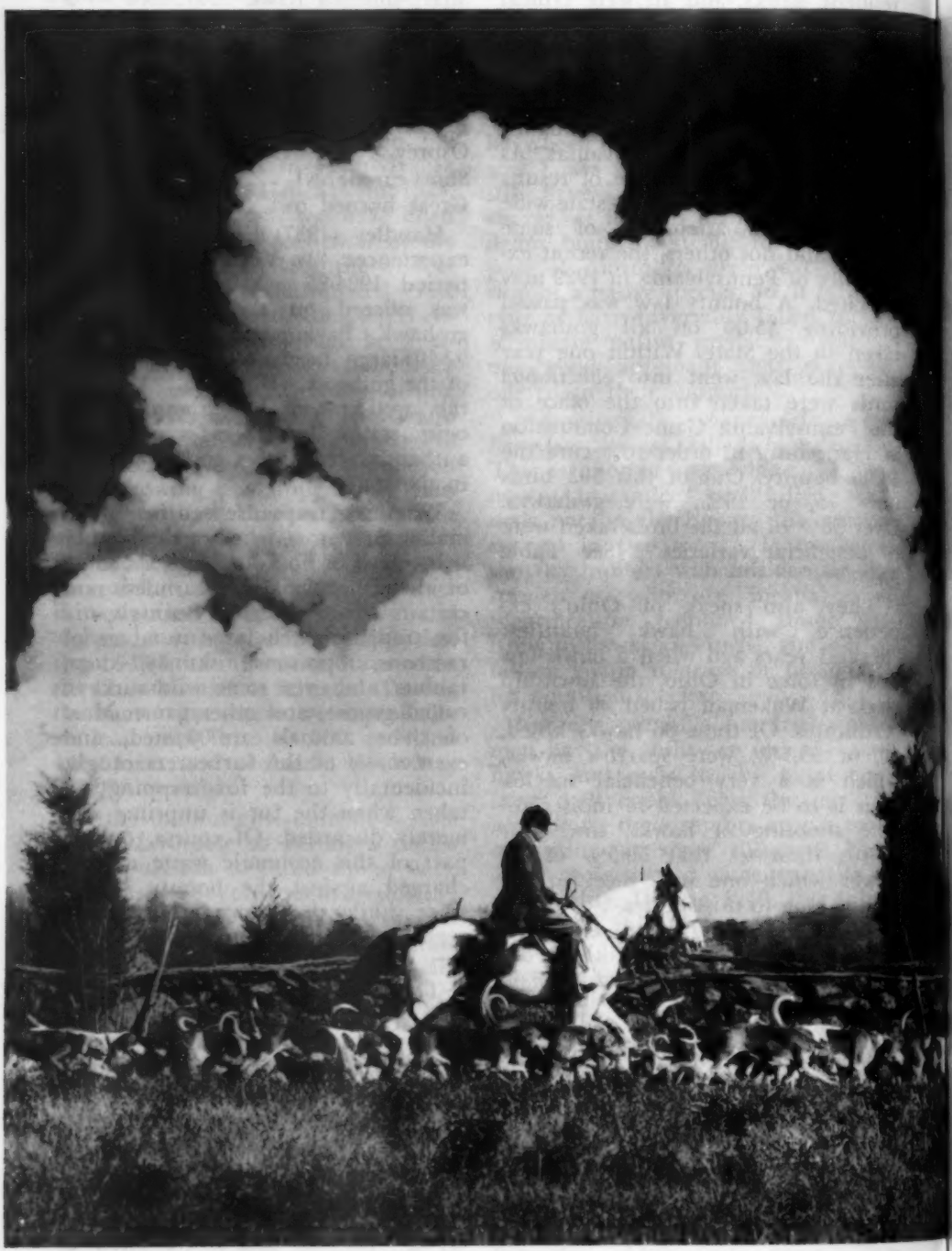
Table 3—Species and number of individuals killed in state-wide eradication campaign against the goshawk in Pennsylvania, 1929 (from Baldwin, Kendeigh, and Franks, 1932).

Red-tailed hawk	165
Cooper's hawk	120
Red-shouldered hawk	84
Goshawk	76
Marsh hawk	28
Sharp-shinned hawk	9
Rough-legged hawk	7
Sparrow hawk	4
Broad-winged hawk	3
Duck hawk	3
Pigeon hawk	1
Osprey	1
Short-eared owl	1
Great horned owl	1

Handley (1937) discusses Virginia's experiences: "In Virginia during the period 1924-29 a state-wide bounty was offered on the head of the goshawk. Payments were made on 9,540 large heads, supposedly those of the goshawk, yet Dr. J. J. Murray, the well-known Virginia ornithologist, states that there is only one authentic record of a goshawk killed in the state."

Wherever traps are set for mammalian predators, whether the bounty is involved or not, other species, some of them beneficial or harmless, are certain to be caught. Pennsylvania fox trappers catch large numbers of raccoons, opossums, skunks, dogs, rabbits, and even some wild turkeys, ruffed grouse, and other game. Most of these animals are wasted, and even many of the furbearers caught incidentally to the fox trapping are taken when the fur is unprime and merely discarded. Of course, only a part of this economic waste can be charged against the bounty system since similar losses occur during the regular harvest of furbearers, predatory or otherwise.

The pole trap set for hawks and owls is also indiscriminate. Most often pole traps are placed to protect concentrations of game or poultry as around game or chicken farms, but there are some who use pole traps to catch hawks or owls for bounty. Unless skillfully placed and baited, pole trapping is not selective, and the beneficial hawks and owls are taken along with the destructive ones. If set lightly enough to take sharp-shinned hawks, small birds of all



Tally-ho! Photo by Wm. M. Rittase

kinds are caught; if set harder, so that small birds are safe, the large *Buteos,* the predominantly beneficial group, will be caught. Wight (1931) in speaking of the use of pole traps says: ". . . it seems wise to limit carefully the use of pole traps to those areas where game is concentrated in unnaturally large numbers, such as at game farms, or where it can be definitely established that damage of a serious nature is being done by species which can best be controlled by these devices."

There are those who believe that bounties are not only at fault in causing the indiscriminate killing of innocent species but also in causing the non-selective destruction of innocent individuals within a condemned species. Hausman (1927) defends this position: "If one should see a man in a blue suit making his escape after having robbed the house, and should thereupon sally forth into the street with a shot-gun and blaze away at every man in a blue suit that he happened to meet, he would be carrying out in practice the principle upon which many act when they wage indiscriminate warfare upon our native hawks." In other words, a state-wide bounty may cause the destruction of predatory animals in regions of the state where, because of varying faunal patterns, the species may be incapable of material damage. And too, even in areas where damages to livestock or game is evident, this destruction may be confined to the activities of a few individuals of a species. The bounty, however, is the same price for both the innocent and the guilty.

Inefficient—bounties paid on animals killed accidentally or incidentally. This is one of the strongest arguments against the bounty system, and, for certain species in certain regions, it is sufficient reason for abolishing bounty payments altogether. Even the most staid protagonists of the county system can hardly deny that any sum paid for the elimination of a predator which would have been killed anyway is a waste of money. Some say that this may help repay those who have lost livestock to predators, but, at least from a game management viewpoint, it is wasted money.

What proportion of the total number of predatory animals taken are killed accidentally, incidentally, or in defense of personal property? This of course, depends upon the abundance of the species, the extent of its distribution, whether it is easy or difficult to trap or shoot, and whether it occurs in heavily or lightly populated regions. It should be obvious that fewer coyotes would be killed accidentally or incidentally in Nevada or Idaho than there would be foxes in thickly settled states like New York or Pennsylvania.

Latham (1951), in a study of Pennsylvania's bounty system for the fiscal years from 1948 to 1950, found that 58 per cent of the claimants for fox bounty presented only one fox; 29 per cent of the claimants presented from two to five foxes; and only 13 per cent had trapped or shot more than five. Only 3.6 per cent of the 6,690 weasel claimants for the 1949-50 fiscal year caught more than ten weasels during the twelve-month period, and about 50 per cent had killed only one weasel. Over 81 per cent of the claimants for horned owl bounty submitted only one owl, and only 2 per cent captured five or more.

The study also revealed that of the total number of foxes submitted for bounty, 73 per cent would have been killed without the added incentive of the bounty payment. Over 75 per cent of the weasels, 59 per cent of the horned owls, and 96 per cent of the goshawks would have been killed whether a bounty had been in force or not.

A certain number of predators are found dead upon highways, or are killed by farm machinery, or, in the

case of weasels, may be brought home by housecats. *These may be bountied, too.*

Another type of inefficiency not generally considered by the opponents of the bounty system is the payment of money for the killing of predatory animals from regions where they are not seriously conflicting with man's economy or man's pleasures. In western states, the removal of coyotes, wolves, or mountain lions from regions that are not utilized for cattle or sheep grazing and are so inaccessible that the hunting possibilities are little exploited may be of little real value. Even in the East, for instance Pennsylvania, there is considerable doubt whether the taking of foxes, weasels, goshawks, and great horned owls from the "big woods" country, which is primarily deer and bear range, actually contributes much to hunting success in those areas. On the other hand, on agricultural land, where the bobwhite quail, ringnecked pheasant, and cottontail rabbit are found in greatest abundance, predator control may be far more efficient because the utilization of game, both by predators and by hunters, is much more intense. Of course, a region in which predators are not controlled may act as a reservoir to keep "controlled areas" continually stocked, but little is known concerning the extent to which this occurs.

Impractical—costs often too high for results obtained. In order for any enterprise to be practical, the return should exceed the output, and whenever a large margin of profit is realized it is considered good business. The elementary question, in regard to the bounty system is—does the expenditure of $10 in payment for the killing of a predatory animal either save $10 plus worth of live- plus worth of game for hunting? It stock or provide an additional $10 is true that the question is elementary, but who can profess the omniscience necessary to answer it?

This "balancing of the books" is a most difficult task. Many critics of Pennsylvania's bounty system state that it is impossible to show that the immense sum spent for the control of predators (over $3,000,000 since 1915) has contributed to an increased kill of game in the state. Since a bounty on predators has been in effect constantly throughout the entire state since 1915, it is much like a scientific experiment without a control—nothing can be proved nor disproved. Consequently, no one can show that the bounty has or has not helped Pennsylvania's hunting. Who can say what it might have been if no bounties had been paid during these years?

There is reason to believe that the control of large predators in the West as a protection to livestock or big game may be a practical undertaking, at least under certain conditions and on certain areas. But there is much less evidence that the control of small predators by means of the bounty as protection for small game is a paying proposition. Even this is a matter of relativity. It is now generally accepted that the artificial propagation and stocking of most game is impractical; but it is still widely used, with crossed fingers, as a means of increasing the game supply. Other management efforts may be impractical. *Therefore, it may not be so much a matter of deciding whether controlling predators by means of a bounty system is practical or not practical, but, instead, whether it is less practical than other commonly used management measures.*

Crissey and Darrow (1949) in reporting upon the predator control experiment on Valcour Island in Lake Champlain, New York, stated that the control efforts produced a substantial increase in numbers of

Photo by W. Bryant Tyrrell

The Bald Eagle, our national emblem, is a bird of prey but lives on fish. The only eagle sanctuary in the United States is located in Pennsylvania on Mt. Johnson's Island in the Susquehanna River near the city of Lancaster.

ruffed grouse and snowshoe hares for three years, but, at the end of that time, disease and possibly other factors caused a marked decline in numbers. They estimated that the same amount of control as practiced upon Valcour Island to produce the temporary increase of game, if applied to the entire state of New York would cost at least $10,000,000 annually.

Conducive to fraud. Wherever or whenever there has been a bounty, there have been attempts to collect payment fraudulently. Sometimes these attempts are made by innocent persons who are ignorant of certain regulations governing the payments of claims or are incapable of making correct identification of predatory animals on the bounty list. But by far the greatest number of the fraudulent claims are made by persons who are aware of their deceit.

Gordon (1923) indicates the extent of fraud in the early Pennsylvania bounty system (1913-1915): "Many justices of the peace, incompetent to identify various species of birds and mammals, prepared certificates to the county commissioners on the strength of a statement made by the claimant. In many instances, justices of the peace passed red squirrels, flying squirrels, and wood rats for weasels; all sorts of animals for foxes; domestic cats of various sizes and colors for wildcats; birds of all kinds, including practically everything from the heads of domestic fowl, gathered up at slaughter houses, to the heads of all species of hawks and owls, even the heads of game birds, for the two hawks and one owl on which bounties were offered by the 1913 law. In a number of other instances, I regret to admit, investigations developed that officials authorized to administer oaths were disposed to do almost anything for a dollar, and with the aid of individuals of low repute made up affidavits and certificates for the killing of vermin of various kinds without a single hair or feather of any sort being presented. Between officials who were imposed upon because of their inability to identify various species and those who deliberately aided in collecting fraudulent bounties, the total amount of money claimed from the hunter's license fund during the twenty-one months the law was in force was more than $350,000."

Handley (1937) cites a somewhat similar experience in Virginia: "As is evident from what has already been said, fraud was rife in the system. Investigation disclosed that not only the scalps of all kinds of hawks were being brought in for bounty, but also the upper bills of chickens and the heads of such protected song and insectivorous birds as the mockingbird, the robin and the bullbat or nighthawk. Trophies from other states were brought into Virginia wholesale for the bounty, in spite of the fact that a sworn statement was requested, declaring that each scalp was of a certain species and was taken in Virginia."

Another instance of fraud in connection with the hawk bounty was reported by LeCompte (1931): "In Dorchester County where the majority of hawks are killed, the natives have a habit of putting the heads in a tin can and placing salt over them which naturally forms a brine within a few days and when they were presented for inspection, it was nearly impossible to tell the species."

Bounty fraud has taken some peculiar twists, and in some cases has shown pronounced ingenuity on the part of the claimant. Hamilton (1946) cites several cases: ". . . Over the years, counties in mid-western states have paid bounties on ground squirrels, which pilfer some grain. Usually the tail only must be presented when the bounty is claimed. A student once told me that the

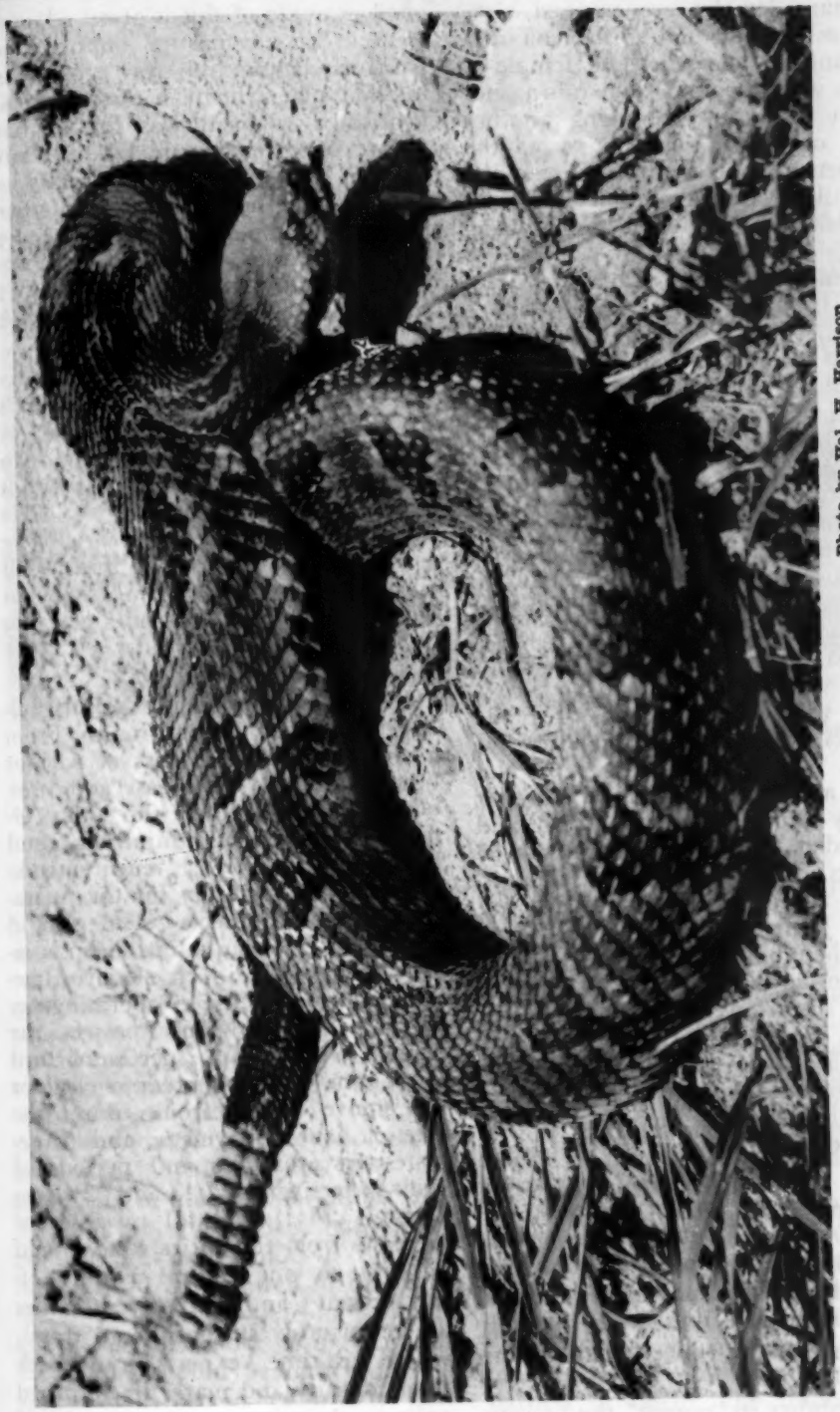


Photo by Hal. H. Harrison

The timber rattler is a predator which respects neither man nor beast.

pregnant females are trapped alive in the spring, the tail cut off and the animal released. The female is in no way impaired from raising her family and thus producing another litter of tailed young ones for the trappers to operate upon. Some unscrupulous trappers even split the tail lengthwise with a razor blade, thus doubling their stakes at the moment the former owner was nursing a litter of young squirrels. . . . In 1937 an investigation was started and it was found that one man sent in 560 coyote pups [at $2 each in Montana]. All of these were skinned, and the pelt was tanned. Critical examination of these pelts revealed them to be gophers. . . . In central Washington during 1925, an investigation disclosed that wildcat skins were being shipped in from Mexico to Texas and then to Washington and British Columbia. The bounty was paid by a girl in the auditor's office who didn't care whether it was a wild cat or a house cat. Some hunters were paid as high as five or six thousand dollars. . . . Not long after this incident another bounty hunter entered the state and proceeded to present for bounty 35 bobcats in one county, 48 in another, 30 in another, and 40 in still another [pelts marked by removing feet when bounty was paid.] Investigation by the county officials, whose suspicions were thus aroused, led to the man's arrest. In his car were 75 bobcats and a sack containing 356 extra bobcat feet. Close examination showed that the feet had been sewn onto some of the skins. . . . Some years ago, cobras became too abundant in India, so officials offered a bounty on the snake. The natives dug up the nests, incubated the eggs in regular hotbeds and successfully raised the young that they might collect bounties on the snakes."

The ability to "outwit" the bounty officials is not confined to adults. A good example of this is given (Anon, 1949): "In the past a bounty was paid on magpie and crow eggs. This method of payment had to be discontinued when it was found that many youngsters would take all but one egg out of the magpie or crow nest on the theory that the mother bird would come back and lay some more, and they would have a continuing source of revenue." And from Douglass and Stebler (1946): ". . . More than one subsequently respectable citizen can recall boyhood excursions to the town clerk's office with a fragrant assortment of crow and woodchuck heads, to reap the bounties thereon. Once the funds were pocketed, the next move was a rapid withdrawal to a point offering a discrete view of the town hall trash can. With luck the specimens would soon be thrown out, ready to be retrieved for bounty another day. . . ."

How can fraud in the bounty system be reduced to a minimum? From a study of the mechanics of various bounty systems, both past and present, it appears that the most efficient in terms of minimized fraud fulfill the following requirements: (1) The responsibility for the operation of the bounty system should be vested in a qualified conservation agency, not in an elective, lawmaking body: (2) the operating organization alone must possess the power to place any species of bird or mammal on the predator list, or to remove it therefrom, to set the rate of bounty payment, and to declare the areas for and periods of their effectiveness (1 and 2 from Gerstell, 1941); (3) all carcasses or all hides from the entire state should be sent to one central bounty office (county and township bounties are notoriously susceptible to fraud) where full-time "experts" can check their identity and mark the returned pelts so that they can be recognized if the claimants attempt to collect

PGC photo by Latham

When pelt prices are low as they are at present for long-haired furbearers, there is little criticism of warm weather trapping.

bounty twice on the same pelt; (4) whenever the validity of a claim is questioned by the trained personnel, there should be adquate provision for full investigation backed by the authority for just and impartial prosecution of all offenders; (5) hawks and owls should be submitted to the central office (where they are destroyed or utilized for scientific studies) within a specified time limit; this restriction precludes the possibility of much importation from other states; and (6) the entire, untanned, but dried, hide of fur animals should be required so that easy identification is possible and importation becomes more costly and difficult; furs should be returned. The system described is essentially that used by the Pennsylvania Game Commission.

Economic waste—furbearers taken when fur is not prime. Some criticism concerning the economic waste caused by the bounty system is deserved. The extent of this waste is usually exaggerated. When fur prices are high on predatory animals for which bounties are being paid, most trappers and hunters of their own volition wait until the furs are prime so that they can reap the double benefits. But when the pelts have little value and the bounty constitutes the principal return, then the hunter or trapper may continue his activities the year around. After all, is there much difference between $5 and $6, especially when furs become prime during the winter months when these animals are hardest to catch? The trapper who can catch 50 foxes in October at $4.50 to $4.75 is better off than the

man who waits until December and only catches 25 to 30 foxes at $5.50 to $6. When furs have little or no value, they cannot be considered an important natural resource, and, temporarily at least, the taking of these animals when pelts are unprime is not a serious economic waste.

Sometimes keen competition between trappers will cause one to start early "to beat the rush," and then the others are likely to follow suit in an effort to get their share. Such matters can often be straightened out by the trappers themselves if they show a willingness to cooperate.

The Control of Domestic Predators

It is ironical that many of the men who are most vociferous in damning wild predators are at the same time guilty of permitting their own household pets—their cats and dogs—to run at large and kill game whenever the opportunity presents itself. The roaming dog and the hunting cat are among the most destructive of all predatory animals and their combined depredations upon livestock and game probably equals that of any two wild predatory species in most of the heavily-populated states of the East. Any wildlife worker who has many contacts with owners of cats will hear of the wonderful exploits of "Tiger" who "brought 37 young rabbits in to her bunch of kittens this spring" (this is said with a definite show of pride in the cat's hunting ability), and of "Priscilla" who "just catches lots of little birds, but she needs raw meat to keep her coat soft and shiny, doesn't she?" Nearly every life history study of game birds, whether it be on ringnecked pheasants, bobwhite quail, Hungarian partridges, woodcock, ruffed grouse, or others, points to the house cat as one of the chief offenders in killing incubating females and destroying the nests. Its destructiveness to cottontail rabbits, newly hatched game birds, and recently released, artificially propagated game birds needs no emphasis.

Forbush (1916), Pearson (1933), Henderson (1927), and many, many others have made eloquent appeals for the control of the vagrant cat to no avail. Because the general public is suffering from a conservation blindness for which there appears to be no immediate cure, it seems foolish for the writer to add more wasted words to what has already been said. But he should like to leave this thought with the reader: If man is going to continue to ignore the depredations of his domestic animals, over which he possesses the power of complete control, is it fair to condemn and to persecute wild predators, many of which are far less destructive than his cats and dogs, and all of which possess admirable qualities lacking in most of the half-fed, mongrel dogs and cats running at large? Perhaps far fewer wild predators would need to be killed to accomplish the goal of game management—sustained game production for recreational purposes—if the numbers and the activities of cats and dogs, the simplest of all predators to control, were carefully restricted.

Photo Penna. Game Comm.

The barn owl, screech owl, and long-eared owl (pictured above) are three desirable predators which can be encouraged by building nesting boxes and providing thick evergreen cover.

Management of Desirable Predatory Species

Much thought has been given to the values of certain beneficial predators, but few attempts have been made to utilize the services of these animals for the public good. If a few barn owls or screech owls scattered here and there are of such material benefit in the reduction of the numbers of rodents, why should not twice that many or ten times that many perform a proportionately greater service for mankind?

Many wildlife workers have suggested the management of desirable predators. Adams (1925) states: ". . . The proper use of predators in the areas of extensive agriculture is probably today one of the most important predatory problems needing careful study. In the less extensively cultivated areas the predatory animals will not only do relatively little harm, but they can do positive good in controlling rodents, and in providing an annual crop of furs; and it is in just such conditions that we should consider giving them all the protection possible . . ." And Bailey (1918) adds: "If the Sparrow Hawk or Screech Owl were not only managed but propagated they would do more in the way of ridding us of insect pests and other vermin, such as mice, etc., than all the cats in the vicinity."

Some suggestions have been made for management techniques. Emlen and Glading (1945) suggest nesting shelters: ". . . Studies have shown that a single barn owl can take more than 4,000 mice from its beat in the course of a year. Such a bird should be rigidly protected and even encouraged on a quail range. Roofed wooden boxes or small barrels provided with a 4- or 5-inch entrance hole make excellent shelters and nesting sites for barn owls when placed on poles or wired in trees at 10 to 15 feet above the ground. The establishment of such boxes helps in quail conservation."

Allan (1942) cites a case where predator management was actually practiced: ". . . An instance is known to the writer in which a Pennsylvania orchardist was able to attract many screech owls to his land by furnishing bird boxes. During one year he had 13 or 14 pairs using the boxes, and was satisfied that they had an appreciable effect on the mouse population. Sparrow hawks, barn owls, and barred owls might be attracted in the same way. He also captured black snakes and other non-poisonous species and released them in the orchard, although the success of this measure is unknown. Skunks also were protected by this orchardist and various shelters such as tiles were provided for them."

He continues: "Bond [Bond and Borell, 1939] states that the Soil Conservation Service advocates the erection of poles with cross perches in treeless alfalfa fields to attract barn owls for the control of meadow mice; while Leopold (in conversation) suggested small plantings of cottonwoods, well scattered in the Plains area, to attract nesting hawks and great horned owls. E. Lowell Sumner, Jr., in a letter, tells of a relationship of eucalyptus growth to barn owl populations of considerable value. Hedgerows of tall, dense-topped trees were found to harbor large numbers of owls, and to provide nesting and roosting sites for red-tailed hawks, sparrow hawks, and screech owls, as well. In a 4-acre woodlot, Sumner noted a relatively stable population of 50 barn owls that persisted until the woodlot was cut down.

"The writer here suggests, for study purposes at least, the possibility of attracting burrowing owls to sites

populated by kankaroo rats. A post-hole digger might serve to start a colony. Cannot weasels, skunks, badgers, raccoons, swift foxes, and other predators of rodents be similarly encouraged?

"From a practical standpoint efforts to increase the animals predatory on rodents probably should be accompanied by measures to expose the prey to them."

Germany became alarmed at the scarcity of hawks and owls, and, with the added scare of a mouse plague in the upper Rhine Valey during 1931 and 1932, established an owl farm where the great uhu, of the same genus as our great horned owl, is being raised and reintroduced into areas from which it had been exterminated (from Pough, 1938).

The few quotations given indicate that wildlife men realize the potential value of beneficial predators, particularly as an aid in the reduction of the numbers of small rodents. Farmers and orchardists should welcome the services of the

Is it fair for man to condemn and persecute wild predators when he ignores the depredations of his domestic cats and dogs?

PGC Photo

forms which live principally upon these small mammals and should encourage them at every opportunity. It is likely that a barn owl will kill more mice and rats around a farm than a half-dozen ordinary house cats, and, unlike the cats, barn owls are seldom destructive to game.

Fifteen Cardinal Points of Predation

1. The term "predator" does not necessarily denote a destructive animal. Some of the animals most beneficial in respect to man's economy are predators.

2. Predators considered most injurious may under certain conditions be decidedly beneficial, and those recognized as harmless or beneficial may at times or in certain places be definitely destructive.

3. The most destructive predators, when occurring only sparsely, can have little effect upon the total numbers of desirable prey species, but an only slightly destructive predatory animal, if it occurs in sufficient abundance, can become a potent decimating agent.

4. Generally speaking, predators live on the annual surplus produced by a prey species, and their influence seldom causes a serious reduction in succeeding breeding populations.

5. Except under the most extenuating circumstances, no predator except man will ever exterminate a prey species.

6. Because animal populations tend to increase toward self-destruction if not held in check by certain counterforces, predation, as one of these reduction factors, may be considered a beneficial service for most prey species. In fact, predators may be an important factor in the survival of some prey species.

7. The net effect of predation upon a particular prey species is measured, not in terms of its per cent occurrence in the predator's diet, but in terms of the numbers lost to predation in relation to the total population of the prey species.

8. Food habits figures for predators have comparatively little significance unless accompanied by specific ecological data concerning both the predator and its prey from the region where the food samples were collected.

9. Predator food habits figures are specific for season, year, and locality, and it should never be construed that a predator's diet for one time or place will apply to any other time or place.

10. Within certain limits, availability, above all else, governs the diet of most predatory animals. The availability of prey animals may vary according to: cyclic influences, weather conditions, pathological or parasitological factors, the amount of protective cover, the adequacy of nutrition, and the introduction of exotic or artifically propagated prey animal.

11. A reduction of the number of predators on a given area does not necessarily mean a reduction in predator pressure on a specific prey animal.

12. Predator control may benefit a fostered species on areas where other environmental conditions are favorable for increase, especially when the numbers of the prey species are well below normal.

13. Predator control may be of value on areas where any considerable part of increase that would normally be utilized by man is being taken by predators. The need or value of predator control in game management is proportional to the intensity of the game harvest.

14. One of the principal stumbling

Photo by Maslowski & Goodpaster

Weasels have bad reputations for killing poultry and small game, but the principal item of diet is mice. The Least Weasel pictured above lives almost exclusively on mice and is a real asset to a farm.

blocks in the way of agreement upon the economics of predation is that most of those who favor predator control are thinking in terms of *individual* animals lost, while most of those who oppose control are usually thinking in terms of *species* or *population* survival.

15. Policies toward predators will always be governed by man's economic and esthetic interests and will seldom be influenced by purely biological reasoning.

BIBLIOGRAPHY

A bibliography of 510 titles was included in the original technical bulletin. Those who are interested in a further study of this subject can obtain this list of references by writing for *The Ecology and Economics of Predator Management.*

PGC Photo by Forbes

The pole-stage forest which now covers many thousands of acres of Pennsylvania's mountains offers little protection to small game against predators.